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REVIEW OF MIOCENE (HEMINGFORDIAN TO CLARENDONIAN) MYLAGAULID RODENTS (MAMMALIA) FROM NEBRASKA

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ABSTRACT

Mylagaulid rodents have been widely recognized in faunas from the Miocene of North America for over 125 years, but a thorough review of the family at the species level has not been done in nearly a century. A large sample of specimens is now available for study from throughout the Miocene section in Nebraska. This sample permits a reexamination of the systematics and phylogeny of this family. It also has allowed for the study of other unique attributes of this family such as sexual dimorphism.

Three subfamilies of mylagaulids are recognized: Mylagaulinae, Mesogaulinae, and Promylagaulinae. The Promylagaulinae are not considered within the scope of this study. The Mesogaulinae are limited to the nominal genus and restricted to the early Hemingfordian. Only two species of *Mesogaulus* are recognized, *M. ballensis* Riggs, and *M. paniensis* (Matthew); only the latter is known from Nebraska. The Mesogaulinae appear both temporally and morphologically ancestral to the later, more advanced mylagaulines.

The Mylagaulinae is comprised of six genera; *Mylagaulus* Cope, *Ceratogaulus* Matthew, *Hesperogaulus* Korth, *Umbogaulus* n. gen., *Pterogaulus* n. gen., and *Alphagaulus* n. gen. *Epigaulus* Gidley is considered a junior synonym of *Ceratogaulus*. All but *Hesperogaulus* are known from Nebraska. *Alphagaulus* is the most primitive and contains species from the late Hemingfordian and early Barstovian. Two species are present in the Nebraska record, *A. vetus* (Matthew) and a new species, *A. tedfordi*. Two other previously described species are referred to this genus, *A. pristinus* (Douglass), and *A. douglassi* (McKenna). The remaining four genera of mylagaulines from Nebraska represent distinct lineages, all of which begin in the Barstovian and continue into the Hemphillian except *Umbogaulus*, which ranges from the late Hemingfordian into the Barstovian only. Three new species are recognized among these genera: *Umbogaulus galushai*, *Ceratogaulus anecdotus*, and *Pterogaulus barbarellae*. *Mylagaulus monodon* Cope is referred to *Umbogaulus*, and *M. laevis* Matthew and *"M." cambridgensis* Korth are referred to *Pterogaulus*. Each of the recognized lineages increases in size through time except *Mylagaulus* and *Umbogaulus*, which decrease in size. It is evident that the presence of nasal horns is not a sexually dimorphic character but defines *Ceratogaulus* as a unique genus as other genera are defined by other forms of ornimentation of the nasal bones.

There is also a biogeographic limitation of these genera. *Ceratogaulus*, *Umbogaulus*, and *Pterogaulus* are restricted to the northern Great Plains; *Mylagaulus* is found only in Florida, northwestern Kansas, and possibly Nebraska. *Hesperogaulus* is present in Barstovian to Hemingfordian faunas from the Great Basin only.

KEY WORDS: Mylagaulidae, Miocene, Biostratigraphy, Phylogeny, Sexual dimorphism, Fossorial

INTRODUCTION

Cope (1878) first named *Mylagaulus sesquipedalis* from the Sappa Creek fauna of Kansas. This species was represented by P^4 (AMNH 8329, later to be named as the holotype) and an isolated incisor and P_4 (AMNH 8330). A few years later, Cope (1881*a*) named an additional species, *Mylagaulus monodon*, from the Barstovian Driftwood Creek fauna of Nebraska (see Voorhies [1990*a*] for age of fauna). The latter species was represented by a partial mandible with P_4 (AMNH

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8327). Later in the same year, Cope (1881*b*) included these unusual rodents in their own family, the Mylagaulidae. Riggs (1899) named a second genus of mylagaulid, *Mesogaulus*, based on a new species, *M. ballensis*, from the Hemingfordian North American Land Mammal Age of Montana.

The first cranial material of a mylagaulid to be described was from Colorado in beds that are now known to be Barstovian in age. Matthew (1901) originally identified this specimen (AMNH 9043) as *Mylagaulus monodon* but later named it as the holotype of a new species, *M. laevis* Matthew (1902). The year after the description of the first skull of *Mylagaulus*, Matthew presented a review of the family. In this review, he described the skull of a mylagaulid from the same horizon as that of the skull of *M. laevis* that had "a pair of large connate processes on the nasals . . . " (Matthew, 1902:291). Matthew named a new genus and species for this skull, *Ceratogaulus rhinocerus*. He suggested the possibility that the unique horn cores of this new skull were a male character of *Mylagaulus*. He rejected this idea in the end because there is no evidence of any marked sexual dimorphism in any other rodents, fossil or Recent (also see Matthew, 1924).

Since Matthew's (1902) review of the Mylagaulidae, five additional genera of mylagaulids have been named. Cranial material is known for four of them: *Promylagaulus* (McGrew, 1941), *Trilaccogaulus* (Nichols, 1976; Korth, 1992), *Epigaulus* (Gidley, 1907; Hibbard and Phillis, 1945), and *Hesperogaulus* (Shotwell, 1958; Korth, 1999*a*). In addition, the skulls of several species of *Mylagaulus* and *Mesogaulus* have been described (Matthew, 1924; McKenna, 1955; Shotwell, 1958; Fagan, 1960; Wilson, 1960; Wahlert, 1974; Galbreath, 1984; Munthe, 1988). Of the genera with known cranial material, only *Epigaulus* has the horn cores on the nasal bones as in *Ceratogaulus*.

It has been the practice in the past to refer isolated cheek teeth and mandibles of mylagaulids from Barstovian to Hemphillian times to a species of *Mylagaulus* if no cranial material is associated. The identification of either horned genus, *Ceratogaulus* or *Epigaulus*, is only done when cranial material with evidence of horns is known. Previously, no dental morphology was used to separate the horned species from the hornless species. In fact, the assignment of the hornless skulls to the genus *Mylagaulus* is completely arbitrary because the holotype of the type species of the genus is an isolated P^4. Hibbard and Phillis (1945) even suggested that the Clarendonian species from Kansas, *Epigaulus minor* (with known presence of horns) and *Mylagaulus sesquipedalis* (type species of the genus), may be synonyms because of their dental similarity and the lack of cranial material of the latter. This suggests that the type species of *Mylagaulus* might have had horn cores, eliminating the previously defined generic difference between *Mylagaulus* and the horned genera.

In Matthew's (1902) review, he also noted the fossorial adaptations of the postcranial skeleton of mylagaulids. All subsequent descriptions of postcranial material of mylagaulines have verified Matthew's observations (Gidley, 1907; Hibbard and Phillis, 1945; Fagan, 1960).

In the century since Matthew's (1902) review of the Mylagaulidae, numerous specimens have been collected from Miocene-aged horizons in Nebraska. The bulk of these were first collected by Ted Galusha and Morris Skinner of the Frick Laboratories in the 1930s through the 1970s. These collections are now housed at the American Museum of Natural History. More recently, beginning in the 1970s, extensive collections of Miocene mammals have been made by M. R. Voorhies and field parties from the University of Nebraska State Museum. These extensive collections contain numerous cranial, dental, and postcranial specimens that are the basis for this study.

The definition of the Promylagaulinae used below follows that of Rensberger (1980). Cranial features of promylagaulines are based on those described by McGrew (1941), Wahlert (1974), Nichols (1976), Munthe (1988), and Korth (1999*b*).

METHODS

Cranial Measurements and Indices.—The placement and orientation of skull measurements are presented in Figure 1. Horn placement index (NHI) is calculated by dividing the distance from the apex of the nasal horn to the anterior edge of the nasal by the total length of the skull. Postorbital process size index (POI) is calculated by dividing the length of the postorbital process on one side of the skull by the minimum width of the postorbital constriction. Cranial width index (W/L) is calculated by dividing the posterior width of the skull by the anteroposterior length of the skull. The angle of the occipital bone (OA) is measured with respect to the plane of the palate. Cranial indices for all mylagaulid species for which they are known are presented in Table 1.

Dental Measurements and Terminology.—Measurements of the premolars of mylagaulids used here represent the maximum width and length of the tooth. The occlusal length was used only in specimens in very late stages of wear where the occlusal measurements are the maximum. Abbreviations for dental dimensions appearing in tables are as follows: a-p, anteroposterior length; tr, transverse width.

The terminology for the fossettes (-ids) of mylagaulid premolars is difficult because different schemes have been proposed by virtually everyone who has worked on this family (Riggs, 1899; McGrew, 1941; Shotwell, 1958; Rensberger, 1979; Munthe, 1988; Korth, 1994). The difficulty with using any system of naming the fossettes is that the homologies of the fossettes are difficult to determine except in very primitive forms that have only a few fossettes that are traceable from the unworn surface of the tooth. Here, the fossettes of the cheek teeth will be referred to only by their position on the tooth (e.g. posterolingual, etc.). The only fossette that appears to be significant in terms of the evolutionary changes in mylagaulids is the anterocentral (or anterobuccal) fossette of P^4. This fossette is forked anteriorly and the separation of the branches of the forked end is a significant character that is used to define genera. In the following text this fossette will be referred to as the *parafossette*. Since the number of fossettes (-ids) on the premolars varies somewhat within a given sample of any one species, the mean number of fossettes, as well as the modal number, are used for comparisons between species and populations (Table 2). Any reference to cusps or styles on the premolars is taken from the terminology of Wood and Wilson (1936).

Reference to early, middle, or late stages of wear on the premolars will be used as defined by Korth (1999*a*); teeth that have been worn to a level within the first 20% of the presumed total height of the tooth are considered to be in early wear, and those in the presumed last 20% of the total crown height are considered to be in a late stage of wear. All others are considered to be in middle or moderate wear (central 60% of the crown height). Clearly, these are approximations. However, the pattern of premolars in early and late wear is distinct (see section on variation in Conclusions); lateral sides of the tooth tilt toward the center of the

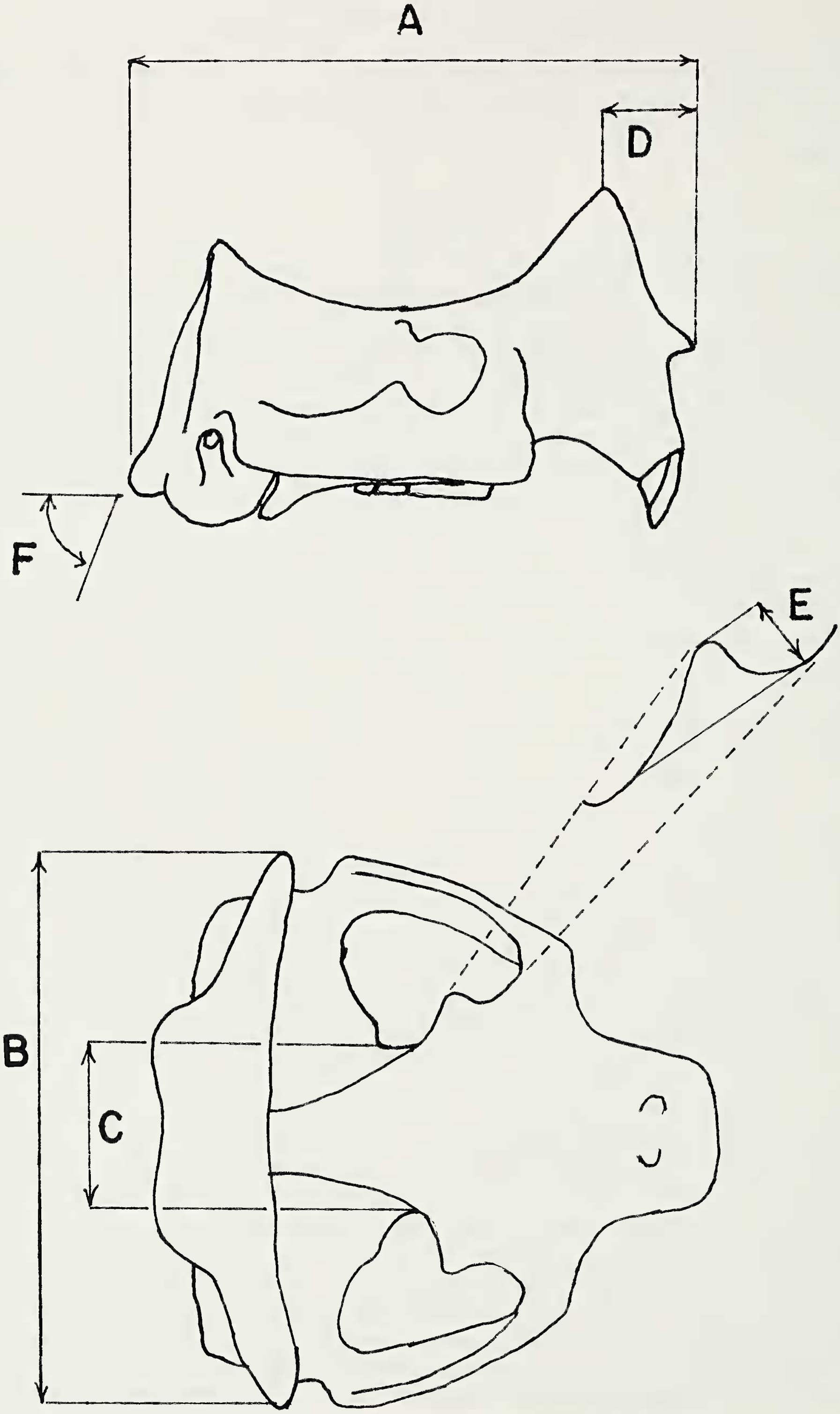
A
D
F
E
B
C

Table 1.—*Cranial indices of mylagaulids.*

	W/L	POI	NHI	OA
Trilaccogaulus lemhiensis	0.46	0.27		110°
Galbreathia novellus	0.52	0.24		90°
Mesogaulus paniensis	0.82	0.32		90°
Alphagaulus vetus	0.77–0.83	0.26–0.36		60°–75°
Alphagaulus pristinus		0.31		79°
Alphagaulus tedfordi	1.22	0.25		90°
Umbogaulus galushai	0.87	0.35		75°
Umbogaulus monodon	0.87	0.35–0.36		75°
Ceratogaulus rhinocerus	0.95	0.19	0.19–0.21	70°
C. cf. *rhinocerus*	0.85–0.88	0.12–0.15	0.16–0.22	67°–68°
Ceratogaulus minor	0.93	0.12	0.29	62°
Ceratogaulus anecdotus	1.00	0.12	0.30	60°
Ceratogaulus hatcheri	0.95	0.11	0.38	63°
Pterogaulus laevis	0.90–1.04	0.39–0.41		68°–75°
Pterogaulus sp.	0.83–0.90	0.34–0.46		54°–60°
Pterogaulus barbarellae	0.85–1.03	0.40–0.57		52°–60°
Hesperogaulus gazini	0.97	0.31–0.35		55°–57°
Hesperogaulus wilsoni	0.80–0.87	0.22–0.25		50°

occlusal surface in early wear, and strongly away from the center of the tooth in late wear.

Abbreviations for Institutions.—AMNH, American Museum of Natural History, New York, New York; CM, Carengie Museum of Natural History, Pittsburgh, Pennsylvania; FAM, Frick Collections of the AMNH, New York, New York; FMNH, Field Museum of Natural History, Chicago, Illinois; UCMP, University of California Museum of Paleontology, Berkeley, California; UNSM, University of Nebraska State Museum, Lincoln, Nebraska; UOMNH, University of Oregon Museum of Natural History, Eugene, Oregon; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C.

BIOSTRATIGRAPHY

The biostratigraphy of the middle and later Tertiary of Nebraska used below generally follows that presented by Tedford et al. (1987) for the Hemingfordian through Clarendonian. However, there are two instances where this paper deviates from the latter work. First, Voorhies (1990*a*) argued convincingly that the Barstovian-Clarendonian boundary, based on the Nebraska stratigraphic section, should be at the base of the Burge Member of the Valentine Formation as was initially intended in the original definition of the Clarendonian (Wood et al., 1941). This differs from Tedford et al. (1987), who included the fauna of the Burge Member in the latest Barstovian (late-late Barstovian). In the following text, Voorhies' interpretation will be used and the Burge fauna will be included as the early Clarendonian (Fig. 2).

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Fig. 1.—Cranial measurements of mylagaulids. A. Total length. B. Total posterior width. C. Width of postorbital constriction. D. Distance of apex of nasal horn from anterior end of nasal. E. Length of postorbital process. F. Angle of occipital. Cranial indices used in text: NL = D/A; POI = E/C; W/L = B/A.

Table 2.—*Number of fossettes (-ids) on premolars of mylagaulids.*

		$\bar{x}$	Mode	Range
Mesogaulus paniensis	P^4	5.0	5	5–5
	P_4	5.2	5	4–6
Mesogaulus ballensis	P^4	—	—	—
	P_4	4	—	—
Alphagaulus vetus	P^4	6.7	7	5–9
	P_4	5.9	5	5–9
Alphagaulus tedfordi	P^4	6	—	—
	P_4	6	—	—
Alphagaulus pristinus	P^4	6.0	6	6–6
	P_4	5.3	5	5–6
Alphagaulus douglassi	P^4	7	—	—
	P_4	—	—	—
Umbogaulus galushai	P^4	8.3	9	7–9
	P_4	8.4	8	7–11
Umbogaulus monodon	P^4	7.9	8	6–10
	P_4	7.3	7	5–9
Ceratogaulus rhinocerus	P^4	8.0	7	7–10
	P_4	8.2	7	8–10
Ceratogaulus cf. *rhinocerus*	P^4	6.7	6–7	6–8
	P_4	7.1	7	5–9
Ceratogaulus minor	P^4	6	—	—
	P_4	7	—	—
Ceratogaulus anecdotus	P^4	7.5	7	6–9
	P_4	7.4	7	6–10
Ceratogaulus hatcheri	P^4	8	—	—
	P_4	9	—	—
Pterogaulus laevis	P^4	6.5	6	5–9
	P_4	5.7	5	5–7
Pterogaulus sp.	P^4	7.2	8	5–10
	P_4	7.0	6	6–11
Pterogaulus barbarellae	P^4	7.8	8	6–10
	P_4	6.5	6	5–8
Pterogaulus cambridgensis	P^4	7.3	8	6–9
	P_4	7.0	7	6–8

Second, Tedford et al. (1987:fig. 3) figured the "Sand Canyon Beds" as biostratigraphically equivalent to the Olcott Formation. However, the former (based on the fauna from Observation Quarry in Dawes County, Nebraska) appears to be older than the fauna from the type area of the Olcott Formation in Sioux County, and is assumed here to represent an earlier deposit.

The Miocene biostratigraphy of Wyoming was not presented by Tedford et al. (1987), so the position and correlation of the Split Rock fauna (late Hemingfordian) is based on the interpretation presented in Munthe (1988:fig. 3).

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Family Mylagaulidae Cope, 1881
Subfamily Mesogaulinae, **new subfamily**

Definition.—Intermediate-sized mylagaulids; first molar lost with eruption of last permanent premolar; P^3 retained, but cheek teeth higher crowned than in promylagaulines; rudimentary roots present on premolars at advanced stage of

NALMA		STRATIGRAPHY	
Clarendonian	late	Ash Hollow Formation	Merritt Dam Member
	middle		Cap Rock Member
	early	Valentine Formation	Burge Member
Barstovian	late		Crookston Bridge Member
	middle		Cornell Dam Member
	early	Olcott Formation	
		"Sand Canyon Beds"	
Hemingfordian	late	Sheep Creek Formation	
	early	Running Water Formation	
		Marsland Formation	

Fig. 2.—Miocene stratigraphic sequence for the Nebraska section used in this paper. Width of units drawn equally, not intended to represent absolute duration (time) or thickness of section.

wear; P^4 retains outline of mesostyle and parastyle and P_4 retains outline of metastylid (lost in mylagaulines); upper incisor with smooth anterior enamel surface (grooved in mylagaulines); skull not as broad as in mylagaulines, but broader than in promylagaulines (W/L = 0.80); occipital not anteriorly tilted (OA = 90°); single sagittal crest on skull (doubled in mylagaulines); postcranial skeleton with fossorial adaptations.

Included Genus.—*Mesogaulus* Riggs, 1899.

Mesogaulus Riggs, 1899

Type Species.—*Mesogaulus ballensis* Riggs, 1899.

Included Species.—*Mesogaulus paniensis* (Matthew, 1902).

Range.—Hemingfordian of Montana, Colorado and Nebraska.

Diagnosis.—Only genus of the subfamily.

Discussion.—The last published classification of mylagaulids at the species level cited six species of *Mesogaulus* ranging from the Hemingfordian to Barstovian (Korth, 1994:109). However, only two of those species are considered here as species of this genus. *Mesogaulus pristinus* and *M. proximus* from the early Barstovian of Montana (Douglass, 1903) are shown to be synonyms and are referable to a new genus of primitive mylagauline (see below). *Mesogaulus novellus*, from the Hemingfordian of Wyoming and Nebraska (Matthew, 1924; Black and Wood, 1956; Munthe, 1988), was referred to a new genus of specialized promylagauline, *Galbreathia* (Korth, 1999*b*). Finally, *M. praecursor* from the Hemingfordian of Nebraska (Cook and Gregory, 1941) has been shown previously to be a junior synonym of *M. paniensis* (Wilson, 1960). All of the conclusions presented in the following discussions regarding *Mesogaulus* are based on the only two species of the genus recognized here, *M. ballensis* and *M. paniensis*.

In his first description of *Mesogaulus*, Riggs (1899) noted that the morphology of the genus was intermediate between *Mylagaulus* and an ancestral form. *Mesogaulus* has developed cranial, dental, and postcranial features that are clearly mylagauline-like, but are more primitive than any true mylagaulines. The skull, while being posteriorly broadened and generally more robust than that of promylagaulines (Wilson, 1960; Galbreath, 1984; Korth, 1999*b*), has not attained the degree of development of these features found in other mylagaulines. Similarly, the dentition is advanced over that of promylagaulines in hypsodonty and complexity of the occlusal surface, however, P^3 is still retained in adult individuals, a promylagauline feature. Features of the limb bones are similarly developed with the hypertrophy of the forelimb seen in later Tertiary mylagaulines (Galbreath, 1984; Korth 1999*b*).

Mesogaulus is a likely ancestor to later mylagaulines. Its age, early Hemingfordian, is also intermediate between promylagaulines and mylagaulines (see Korth, 1994 for age ranges of promylagaulines). The only exception is the late occurrence of the derived promylagauline *Galbreathia* (Korth, 1999*b*).

Mesogaulus paniensis (Matthew, 1902)
(Fig. 3A, B, 4)

Mylagaulus paniensis Matthew, 1902.
Mesogaulus paniensis (Matthew) Cook and Gregory, 1941.
Mesogaulus praecursor Cook and Gregory, 1941.

Type Specimen.—AMNH 9361, partial mandible with incisor and P_4 (Matthew, 1902:fig. 4).

Referred Specimens.—Additional topotypic specimens listed in Galbreath (1953:95) and Wilson (1960:51–53); referred specimens from Nebraska cited in Cook and Gregory (1941:551) as *Mesogaulus praecursor*; and FAM 65511, nearly complete skull with complete dentition, associated mandibles, and some postcranial bones.

Horizon and Locality.—Topotypic specimens from Quarry A, Martin Canyon beds, Logan County, Colorado; referred specimens from "four miles north of Agate" (Cook and Gregory, 1941:551), Marsland Formation, Sioux County, Nebraska; FAM 65511 from Runningwater Formation, Cottonwood Creek, Dawes County, Nebraska.

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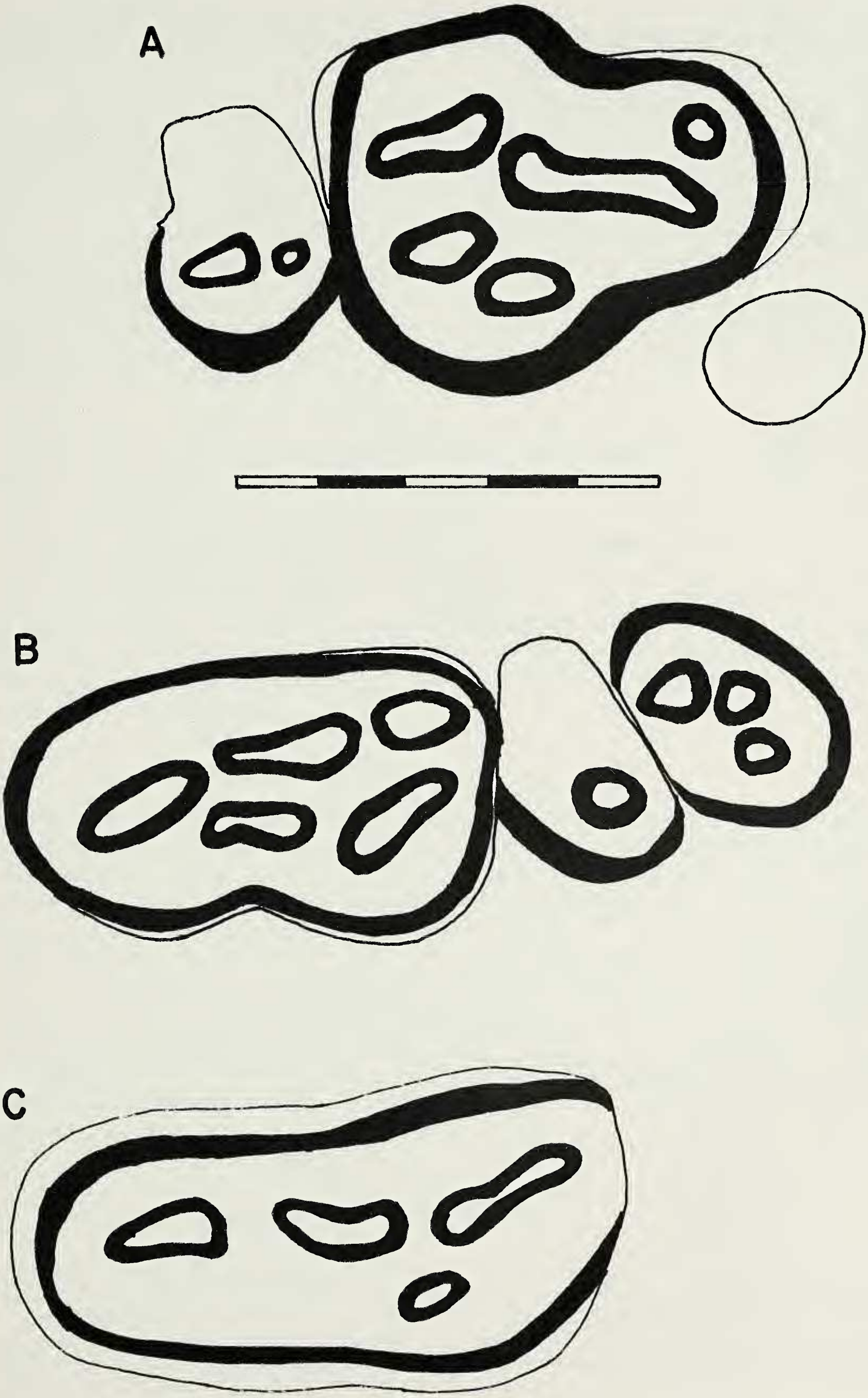
Fig. 3.—Dentitions of species of *Mesogaulus*. A, B. *Mesogaulus paniensis*, FAM 65511. A. P^3– P^4, M^2. B. P_4, M_2–M_3. C. Holotype of *M. ballensis*, FMNH P 25223, P_4.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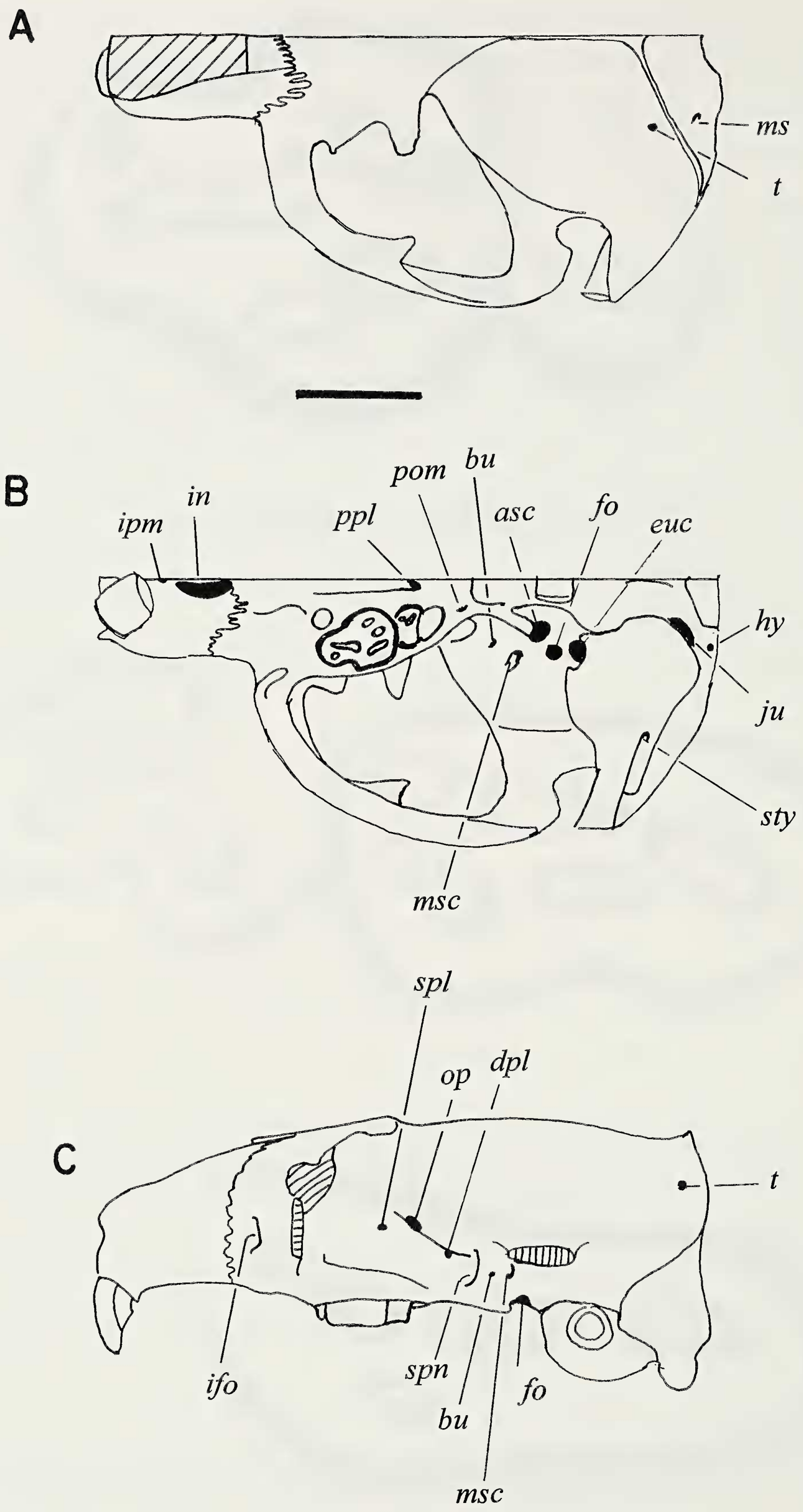
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Age.—Early Hemingfordian (early Miocene).

Emended Diagnosis.—Five or more fossettes (-ids) on P_4, more than in *M. ballensis.*

Description.—Galbreath (1953, 1984) and Wilson (1960) have fully described the dentition of *M. paniensis* along with some skull material and postcranial elements. A nearly complete skull with associated limb elements, FAM 65511, is clearly referable to *M. paniensis*. The skull is generally low, and posteriorly broadened as in mylagaulines, but has not attained the degree of posterior expansion seen in the latter (W/L = 0.82). The postorbital processes are intermediate in size (POI = 0.32) which appears to be primitive for the family. The angle of the occipital is 90°, again a primitive condition, and similar to promylagaulines. However, the positions of all cranial foramina are identical to those of later mylagaulines (Wahlert, 1974:fig. 13).

Dentally, the upper incisors of *M. paniensis* also lack the broad, shallow groove along their medial border that is present in all mylagaulines, and a P^3 is retained in all adult individuals of *M. paniensis* (this tooth is lost in all mylagaulines). The humeri of FAM 65511 are proportioned as in later mylagaulines and are clearly broader than in promylagaulines (Table 3).

Discussion.—In virtually all features of the skull, dentition, and postcranial skeleton, *M. paniensis* is intermediate between promylagaulines and later, more derived mylagaulines. Cook and Gregory (1941) believed that additional specimens of *Mesogaulus* from Nebraska represented a new species, *M. praecursor*, but Wilson (1960) demonstrated that this latter species was a junior synonym of *M. paniensis*. Although Matthew (1902) argued against synonymy, it is possible that the type species of the genus, *M. ballensis* Riggs (1899), is synonymous with the much better represented *M. paniensis* because the former is known only from the holotype, FMNH P 25223, which contains heavily worn cheek teeth (Fig. 3C). This argument cannot be settled until additional topotypic material of *M. ballensis* is recovered and described.

Subfamily Mylagaulinae Cope, 1881*b*

Definition.—Large mylagaulids; P^3 absent; last premolar greatly enlarged (more than twice the size of molars); at least first molars lost with eruption of permanent premolars; no evidence of roots on premolars; upper incisor with broad, shallow groove along medial border of anterior surface of enamel; posterior width of skull nearly equal to anteroposterior length of skull (W/L = 0.77–1.04); occipital tilted anteriordorsally (OA $\leq$ 75°) except in most primitive species; sagittal crest doubled (=parasagittal crests); primitively, small boss of rugose bone present dorsally on anterior end of nasal bones; fossorial adaptations of postcranial skeleton greatly enhanced (ratio of distal width to length of humerus greater than 0.43).

Included Genera.—*Mylagaulus* Cope, 1878; *Ceratogaulus* Matthew, 1902; *Hesperogaulus* Korth, 1999*a*; *Pterogaulus* n. gen.; *Umbogaulus* n. gen.; and *Alphagaulus* n. gen.

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Fig. 4.—Skull of *Mesogaulus paniensis*, FAM 65511. A. Dorsal view. B. Ventral view. C. Left lateral view (zygoma removed). Abbreviations for cranial foramina: asc, alisphenoid canal; bu, buccinator; dpl, dorsal palatine; euc, eustachian canal; fo, foramen ovale; hy, hyoid; ifo, infraorbital; in, incisive; ipm, interpremaxillary; ju, jugular; ms, mastoid; msc, masticatory; op, optic; pom, posterior maxillary; ppl, posterior palatine; spl, sphenopalatine; spn, sphenoidal fissure; sty, stylomastoid; t, temporalis. Diagonal lines indicate broken areas. Bar scale = 1 cm.

Table 3.—*Humeral index (distal width/length) of species of mylagaulids.*

Galbreathia novellus	0.38
Mesogaulus paniensis	0.43
Alphagaulus tedfordi	0.43
Umbogaulus galushai	0.43
Ceratogaulus rhinocerus	0.42–0.45
Ceratogaulus minor	0.45
Ceratogaulus hatcheri	0.44
Pterogaulus laevis	0.43–0.44
Pterogaulus sp.	0.45

Alphagaulus, new genus

Type Species.—Mylagaulus vetus, Matthew, 1924.

Referred Species.—Alphagaulus pristinus (Douglass, 1903), *A. douglassi* (McKenna, 1955), and *A. tedfordi* n. sp.

Range.—Late Hemingfordian of Wyoming and Nebraska; early Barstovian of Nebraska and Montana.

Diagnosis.—Range in size from the smallest to intermediate-sized mylagaulines; skull not as wide posteriorly as other mylagaulines (W/L = 0.77–0.83); low bosses of rugose bone at anterior end of nasals; postorbital process intermediate in size (POI = 0.25–0.35); premolars simpler than other mylagaulines—fewer fossettes (minimum of five fossettids on P_4); P^4 parafossette remains forked until very late wear stage.

Discussion.—In morphology of the skull and dentition, as well as temporal occurrence (late Hemingfordian to early Barstovian), *Alphagaulus* is transitional between *Mesogaulus* and more advanced mylagaulines. In overall size and the morphology of the parafossette on P^4, the species of *Alphagaulus* appear to be divisible into two groups. Both *A. vetus* (Matthew, 1924) and *A. pristinus* (Douglass, 1903) are more gracile, and the buccal branch of the parafossette on P^4 separates from the rest of the fossette in very late stages of wear. *Alphagaulus douglassi* and the new species described below have much more robust skulls than the former species and the lingual branch of the parafossette on P^4 separates first at an earlier stage of wear. These differences suggest possible ancestral relationships to specific later, more derived mylagaulines.

In addition to the two species of this genus recognized from Nebraska, two previously described species are referred here to *Alphagaulus* as well. Douglass (1903) based the species *Mylagaulus? pristinus* on a single mandible with a newly erupted P_4 (CM 742). However, he sectioned the premolar at the level of its maximum dimensions, providing a view of the premolar at an advanced stage of wear for comparison with other species (Fig. 6E). *Alphagaulus pristinus* differs from all other species of the genus in being smaller in size. In the same article, Douglass (1903) described an additional species, *Mylagaulus proximus*, from the same horizon as *A. pristinus*. It was also based on a single specimen, CM 843, a mandible with dP_4-M_3 with an erupting P_4. This specimen is nearly identical to the holotype of *A. pristinus* in size and morphology (Douglass, 1903:189–190, fig. 27). Therefore, *M. proximus* is believed to be a junior synonym of *A. pristinus*.

Alphagaulus pristinus most closely approaches *A. vetus* in size and morphology. Now that a sufficient number of specimens of both of these species is known

Table 4.—*Measurements of premolars of* Alphagaulus vetus *from different areas. Topotypic material is from Sheep Creek Formation of Nebraska. *Split Rock data from Munthe (1988:table 2), no ranges were given. Statistical abbreviations:* n, *number of specimens;* x̄, *mean; OR, size range;* s, *standard deviation;* cv, *coefficient of variation.*

		n	x̄	OR	*s*	*cv*
Late Hemingfordian (Split Rock, Wyoming)*						
P^4	a–p	3	7.4	—	0.4	4.8
	tr	3	5.7	—	0.3	5.1
P_4	a–p	4	8.2	—	1.1	13.4
	tr	4	4.3	—	0.3	6.7
Late Hemingfordian (Sheep Creek Formation, Nebraska)						
P^4	a–p	4	7.8	7.5–8.0	0.2	2.6
	tr	5	5.2	5.0–5.6	0.2	4.3
P_4	a–p	12	8.1	7.3–9.3	0.7	8.2
	tr	12	4.6	4.1–5.2	0.3	7.3
Early Barstovian (Observation Quarry, Nebraska)						
P^4	a–p	15	8.0	7.3–9.0	0.5	6.6
	tr	15	4.7	4.7–6.1	0.4	7.8
P_4	a–p	31	8.4	6.9–9.3	0.6	7.6
	tr	31	4.4	3.3–5.6	0.5	12.0

(Table 4; Sutton and Korth, 1995:table 3); it is evident that *A. pristinus* is indeed smaller than representative samples of *A. vetus.*

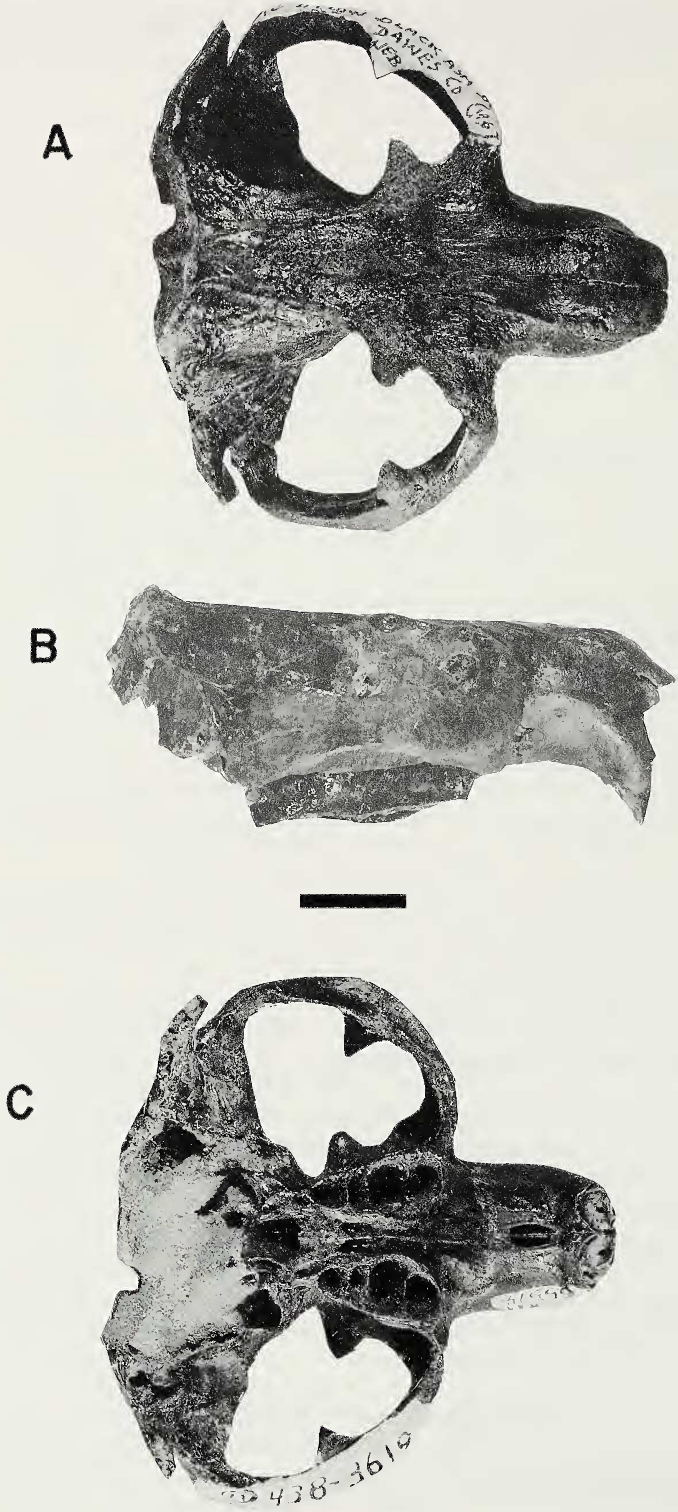
A partial skull from the Barstovian of Montana, AMNH 21307, is assigned to *A. pristinus* based on size and occurrence. It is smaller than skulls of *A. vetus* (width of occipital slightly more than half that of skulls of *A. vetus*), but the angle of the occipital (OA = 79°) and relative size of the postorbital processes (POI = 0.31) are very similar to these measurements in skulls of the type species. The sagittal crest is also doubled as in skulls of *A. vetus.*

Alphagaulus pristinus is restricted to the early Barstovian of Montana. Although Black (1961) and Sutton and Korth (1995) referred specimens from this area to other species (*Mesogaulus paniensis* and *Mylagaulus vetus*, respectively) they are all clearly referable to *A. pristinus.*

Alphgaulus douglassi is represented by a single specimen, UCMP 44694, a partial skull with cheek teeth (McKenna, 1955:fig. 1). This species is also referable to *Alphagaulus.* The major difference between *A. douglassi* and the other species is in the separation of the lingual fork of the parafossette on P^4 (buccal fork separates in *A. vetus* and *A. pristinus*). This separation apparently occurs at an earlier stage of wear than in *A. vetus.* McKenna (1955) noted that the skull of *A. douglassi* had longer parietals than other known species of mylagaulids. This clearly indicates that the angle of the occipital is nearly vertical, as in *A. vetus*, although the posterior end of the skull is missing on the only known specimen of *A. douglassi.* In more derived mylagaulines, the parietals are shortened by the anterior tilting of the occiptal bone. The skull of *A. douglassi* is very robust and has a single, broad sagittal crest, unlike that of *A. vetus* and all known mylagaulines that have a doubled sagittal crest.

Alphagaulus vetus (Matthew, 1924)
(Fig. 5, 6A–D; Table 4)

Mylagaulus vetus Matthew, 1924.
Mesogaulus vetus (Matthew) Cook and Gregory, 1941.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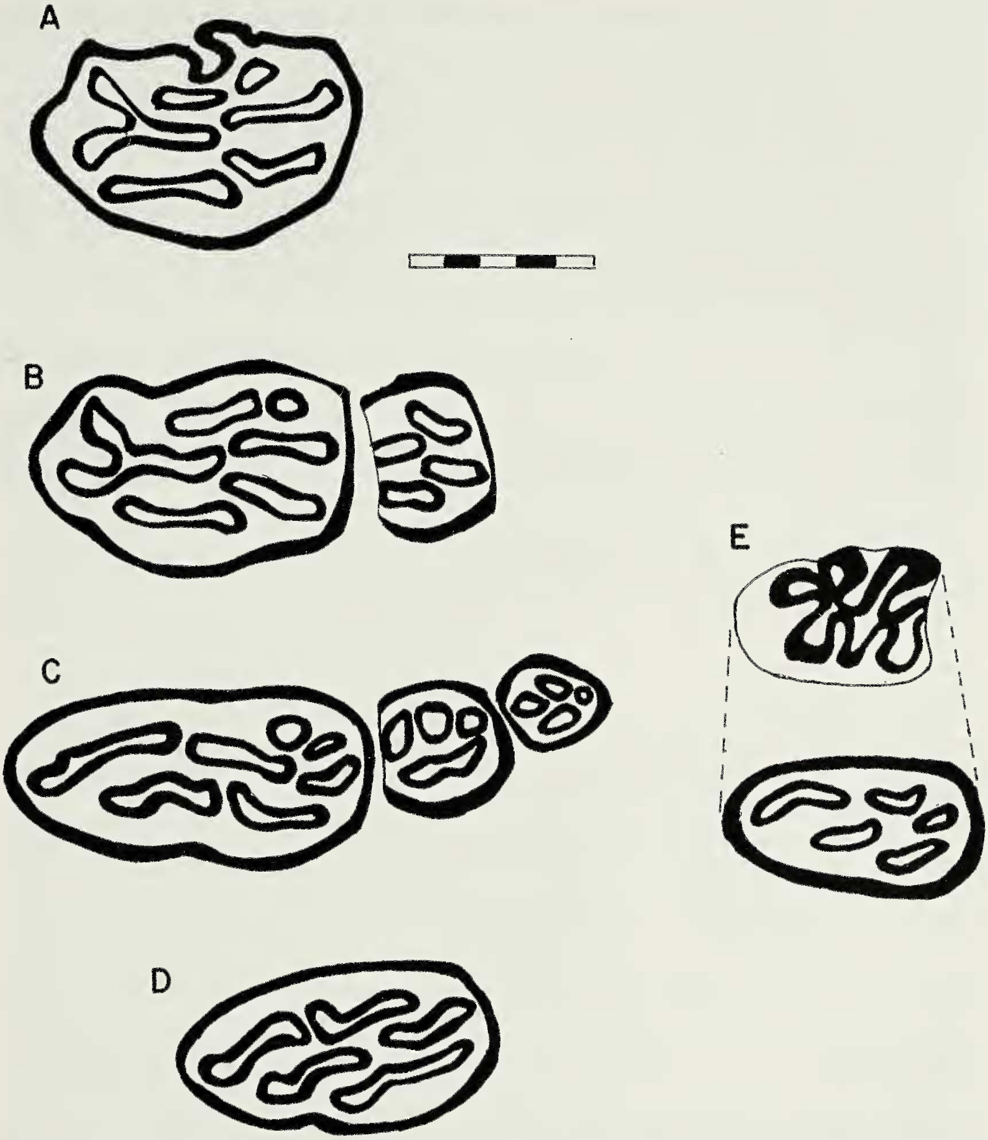

Fig. 6.—Dentition of *Alphagaulus vetus* and *A. pristinus*. A–D. *Alphagaulus vetus* from early Barstovian Observation Quarry, Nebraska. A. FAM 65547, left P^4. B, C. FAM 65536. B. left P^4, M^2. C. left P$_4$, M$_2$–M$_3$. D. FAM 65542, left P$_4$. E. *Alphagaulus pristinus*, holotype, CM 742, little-worn occlusal surface (above) and surface of cross section at midheight of tooth (below). Bar scale = 5 mm.

←

Fig. 5.—Skull of *Alphagaulus vetus*, FAM 65514. A. Dorsal view. B. Lateral view. C. Ventral view. Bar scale = 1 cm.

Type Specimen.—AMNH 18905, right mandible with incisor and P_4, M_2 (Sutton and Korth, 1995:fig. 3H).

Referred Specimens.—Topotypic specimens: AMNH 20504, 20507, 90734; FAM 65515, 65517–65520, 65523, 65526, 65527. From Observation Quarry: FAM 65532, 65534–65536, 65538–65551, 65556, 65558, 65559, 65561. Also see Munthe (1988:24) for list of referred specimens from Split Rock fauna.

Horizon and Locality.—Holotype and some referred specimens from the late Hemingfordian Thompson Quarry, Sheep Creek Formation of Sioux County, Nebraska; other referred specimens from the late Hemingfordian Split Rock local fauna of Wyoming and the earliest Barstovian Observation Quarry, Dawes County, Nebraska.

Age.—Late Hemingfordian to early Barstovian (late-early to early-middle Miocene).

Emended Diagnosis.—Larger than *A. pristinus*; skull not as deep (dorsoventrally) or robust as in *A. douglassi* and *A. tedfordi*; in late stages of wear buccal branch of parafossette of P^4 separates from the remainder of the fossette (lingual branch separates in *A. douglassi*).

Description.—The proportions of the skull of *A. vetus* are intermediate between that of *Mesogaulus* and later mylagaulines. In general, the skull is low and broad as in all mylagaulines (W/L = 0.77–0.83; similar to that of *Mesogaulus*) but is not as posteriorly expanded as other mylagaulines (W/L ≥ 0.88). Similarly, the angle of the occipital (OA) ranges from 60° to 75°, much less than in *Mesogaulus* (OA = 90°) but not as low as in advanced mylagaulines where the angle is as low as 50° (Table 1). The postorbital process is intermediate in size (POI = 0.26–0.36), similar to that of *Mesogaulus*.

A small bump is present on the nasal bones at their anterior end. It is variable in size but is present on specimens that preserve the nasals from the late Hemingfordian and early Barstovian as well. All other features of the skull and mandible are similar to those described by Munthe (1988) for the species, and by Wahlert (1974) for the family.

The number of fossettes on the upper premolar varies from five to nine. The majority of specimens (80%) have six or seven ($\bar{x}$ = 6.7, mode = 7). The largest fossette is the parafossette, which remains forked until very late stages of wear. Of the over 20 specimens examined, only two showed the separation of the buccal branch of the parafossette. Both of these specimens were in very late stages of wear. The remainder of the fossettes on P^4 follow a basic pattern: two on the anterior half of the tooth (one buccal and one lingual to the parafossette); and three on the posterior half of the tooth, roughly aligned with the three on the anterior half of the tooth. The seventh fossette is usually a small, circular one along the buccal edge of the tooth near its center. Heavily worn specimens often eliminate one or more of these fossettes, reducing their number. Specimens with more than seven fossettes appear to be the result of one of the larger fossettes dividing into two or more smaller fossettes.

The lower premolar also consists of anteroposteriorly elongated fossettids, typical of mylagaulines. The number of fossettids ranges from nine to five ($\bar{x}$ = 5.9, mode = 5). As with the upper premolars, the number of fossettids generally is reduced with age. Those specimens with more than five or six fossettids are usually younger individuals. The specimens that are at a moderate stage of wear usually have only five or six. Again, as with the upper premolars, additional fossettids on P_4 are produced by the splitting of one or more of the larger fossettids into two. There is a general pattern in the location of the five main fossettids: three along the lingual edge of the tooth, and two along the buccal side of the tooth.

Discussion.—*Alphagaulus vetus* is the best represented species of the genus. It is also one of the best represented species of mylagaulines. There is virtually no difference in the size ranges and morphology of the samples of *A. vetus* from the late Hemingfordian of Wyoming and Nebraska and the early Barstovian of Nebraska (Table 4). The size of the boss at the anterior end of the nasals varies somewhat, but is always present on specimens that preserve the nasals. *Alphagaulus vetus* is slightly larger than *A. pristinus*. In a very late stage of wear of P^4, the buccal branch of the parafossette separates from the rest of the fossette, unlike *A. douglassi*. This only occurs in very few specimens, all of which are of senile individuals.

Alphagaulus vetus is morphologically intermediate between *Mesogaulus* and later, more advanced mylagaulines in the construction of the skull. The skull of *A. vetus* is broader and has a lower angle of the occipital than *Mesogaulus*, but is not as broad as in other mylagaulines and has a steeper occipital angle. The dentition is also intermediate, having a greater number of fossettes (-ids) on the premolars than *Mesogaulus* but fewer than other mylagaulines.

Alphagaulus tedfordi, **new species**
(Fig. 7, 8, 9B, C)

Type and Only Specimen.—FAM 65711, nearly complete skeleton.

Dental Measurements of Holotype.—P^4, a-p 7.50 mm, tr 5.70 mm; P_4, a-p 6.74 mm, tr 5.40 mm.

Horizon and Locality.—Hot Springs drainage system (below level of Observation Quarry), NE ¼, SE ¼, section 4, T31N, R47W, Dawes County, Nebraska.

Age.—Latest Hemingfordian or earliest Barstovian.

Diagnosis.—Slightly larger than *A. douglassi*; skull robust with vertically oriented occipital (OA = 90°); lingual fork of parafossette on P^4 separates first (as in *A. douglassi*); P^4 retains outline of mesostyle, not becoming completely oval as in other species.

Etymology.—Patronym for R. H. Tedford.

Description.—The postcranial skeleton is similar to that of other mylagaulines with robust limbs, especially the forearms and manus. The ratio of distal width to length of the humerus is within the range that of other mylagaulids (Table 3). The skull is also robust and retains a number of features of *Mesogaulus*. The angle of the occipital is 90°, as in *Mesogaulus* and the promylagaulines (Table 1) and the postorbital process is primitively intermediate in size (POI = 0.25). However, there are a number of features of the skull that make this specimen clearly a mylagauline. The skull is wider posteriorly than in *Mesogaulus* and most other mylagaulines (W/L = 1.22) and there are bosses of rugose bone on the anterior ends of the nasals. These bosses are larger than those of *A. vetus*, but considerably smaller than those of *Umbogaulus* (described below). There appears to be no difference between the arrangement of sutures or foramina on the skull of *A. tedfordi* and of other mylagaulines. The auditory bullae have the characteristic elongated external meatus of all mylagaulids.

The upper premolar of the type specimen is in a moderate stage of wear and has six fossettes; four elongated fossettes (two on the anterior half, two on the posterior half), and a minute buccocentral fossette. The lingual branch of the parafossette has separated to form the minute seventh fossette. This arrangement of the major fossettes is very similar to that of *Mesogaulus* and advanced promylagaulines. The separation of the lingual branch of the parafossette is characteristic of *A. douglassi* (Fig. 9A) and all species of *Ceratogaulus* and *Mylagaulus*. The occlusal outline of P^4 retains the outline of the mesostyle, a character of *Mesogaulus* and promylagaulines.

The lower premolar has six fossettids, reminiscent of the premolars of *A. vetus*, but is much more robust than the latter. Both the upper and lower premolars are wider relative to length than in *A. vetus*.

Discussion.—*Alphagaulus tedfordi* retains a number of primitive *Mesogaulus*-like characters of the skull and dentition. The angle of the occiptial is vertical and the postorbital processes are intermediate in size, as in *Mesogaulus*. Similarly, the outline of the mesostyle is preserved on P^4, another primitive character for mylagaulines. However, the posterior widening of the skull of *A. tedfordi* is much greater than that of *Mesogaulus* and promylagaulines, and the presence of bumps on the nasal bones is also a mylagauline trait.

Alphagaulus tedfordi more closely resembles *A. douglassi* than the other species of the genus. Both *A. tedfordi* and *A. douglassi* are more robust than *A. vetus* and *A. pristinus*, and the lingual branch of the parafossette on P^4 separates at an

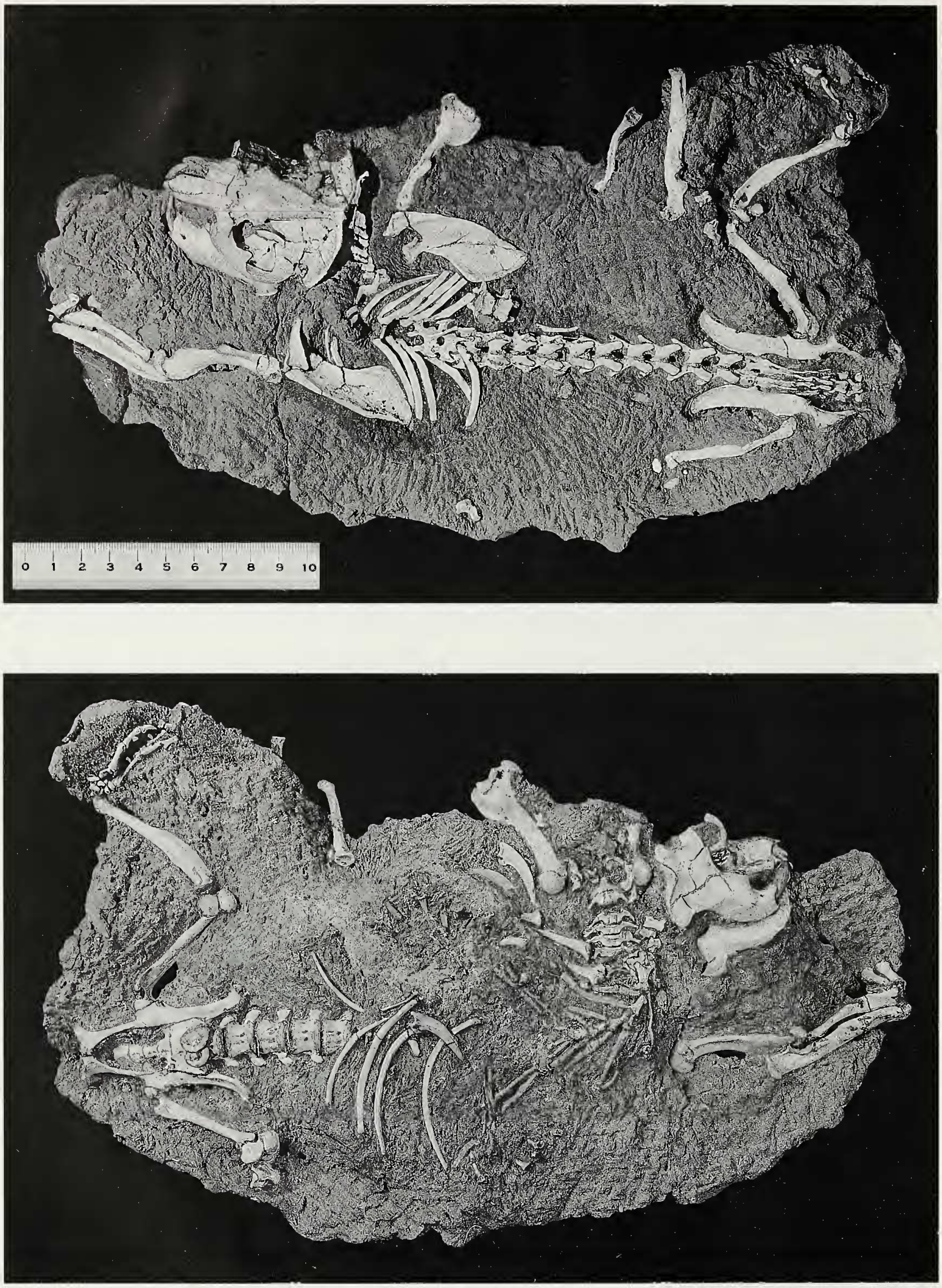

Fig. 7.—Photograph of skeleton of *A. tedfordi*, holotype, FAM 65711. Dorsal view above, ventral view below. Scale is in cm.

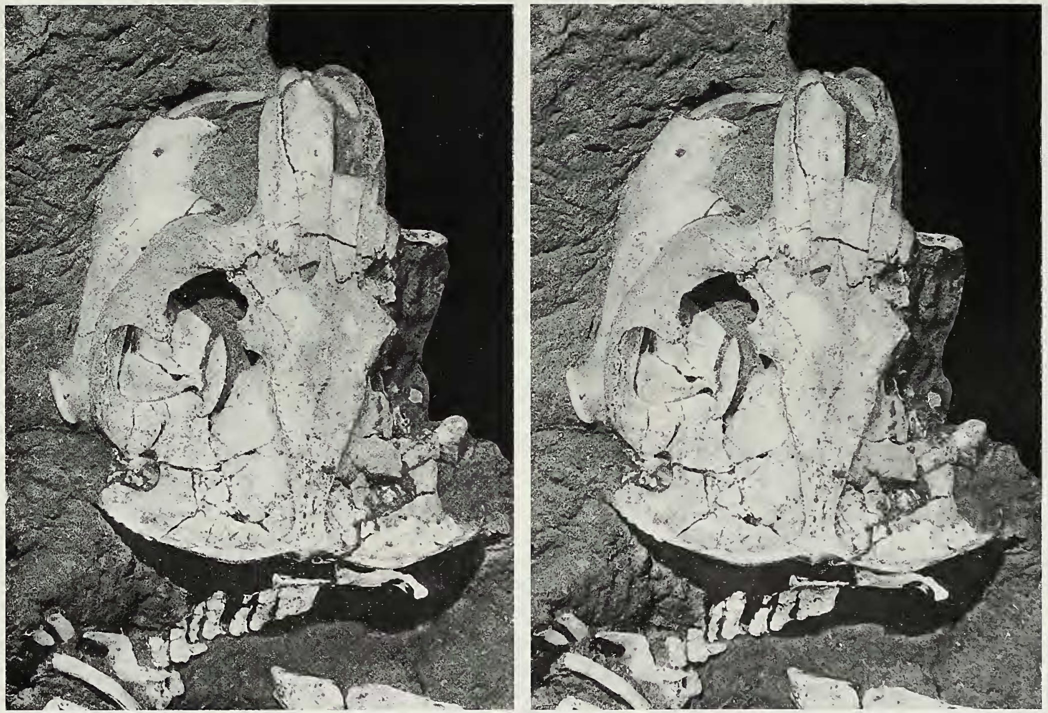

Fig. 8.—Stereo photograph (dorsal view) of skull of *A. tedfordi*, holotype, FAM 65711. Scale = 1 cm.

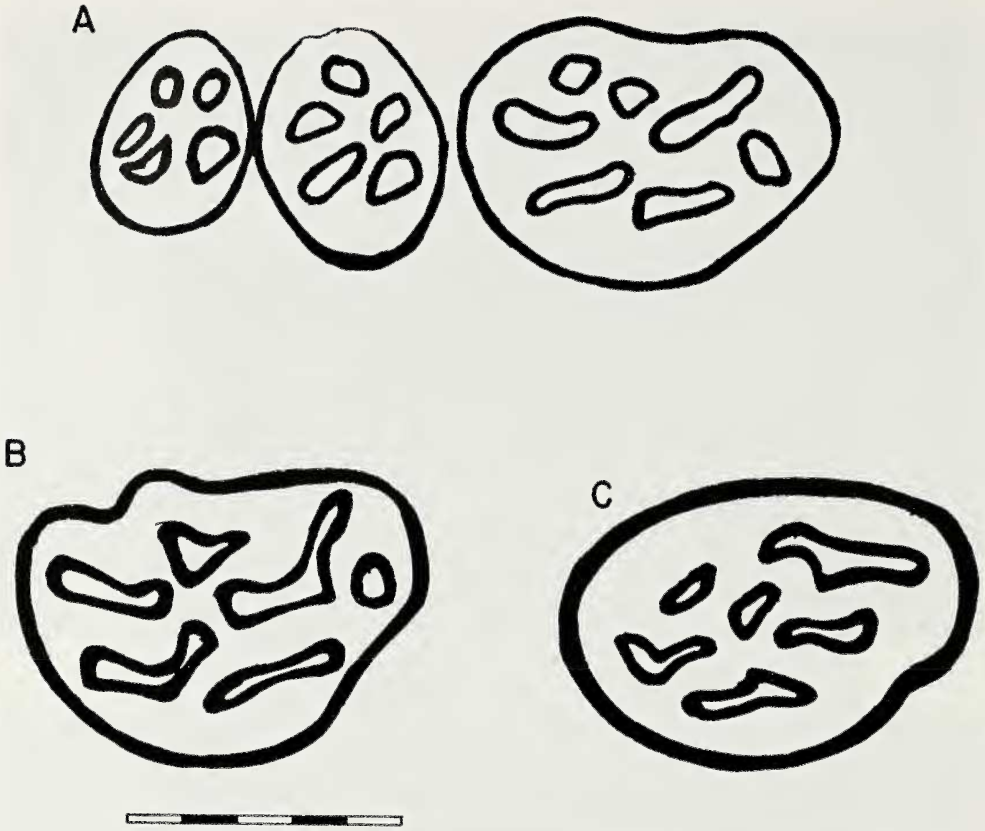

Fig. 9.—Dentitions of the holotypes of *Alphagaulus douglassi* and *A. tedfordi*. A. *Alphagaulus douglassi*, UCMP 44694, P^4, M^2–M^3. B, C. *Alphagaulus tedfordi*, FAM 65711. B. Right P^4. C Right P_4. Bar scale = 5 mm.

earlier stage of wear. *A. tedfordi* can be distinguished from *A. douglassi* by its slightly larger size and the retention of the outline of a mesostyle on P^4.

The more robust skull and separation of the lingual rather than the buccal fork of the parafossette on P^4 in *A. tedfordi* and *A. douglassi* suggest primitive positions of these species with respect to later species of *Ceratogaulus* that share these same characters. The small bosses on the nasals can also be considered primitive to the nasal horns of *Ceratogaulus*. The nasal bosses on a new genus, *Umbogaulus* (described below), are much larger than those of *A. tedfordi* and the premolars have many more fossettes (-ids) than the latter, distinguishing it from *Umbogaulus*.

Umbogaulus, new genus

Type Species.—*Umbogaulus galushai* n. sp.

Referred Species.—Umbogaulus monodon (Cope, 1881*a*).

Range.—Late (and possibly early) Barstovian of Nebraska.

Diagnosis.—Larger than species of *Ceratogaulus*; large bosses on anterior end of nasals; premolars circular to oval in occlusal outline with multiple minute fossettes (-ids), more complex than *Ceratogaulus*; branches of parafossette of P^4 remain attached until very late stages of wear; anterocentral fossettid of P_4 usually anteriorly forked or widened.

Etymology.—Greek, *umbos*, knob or boss; and *gaulos*, bucket.

Discussion.—*Umbogaulus* differs from *Ceratogaulus* in the presence of large bosses at the anterior end of the nasals rather than paired conical "horns." Dentally, *Umbogaulus* has a greater number of fossettes complexity on the premolars than even the most advanced Hemphillian species of mylagaulines. The greatest difference in the premolars of advanced species of *Ceratogaulus* and *Umbogaulus* is that the premolars of *Ceratogaulus* are relatively longer compared to width than are those of *Umbogaulus*, and all the fossettes (-ids) are narrow, nearly straight, and anteroposteriorly oriented. In *Umbogaulus* the fossettes are often rounder and the teeth are relatively much wider (P^4 nearly round in occlusal outline).

Umbogaulus galushai, **new species**
(Fig. 10, 11A; Table 5)

Type Specimen.—FAM 65576, left P_4.

Referred Specimens.—FAM 65571–65575, 65590–65592, isolated premolars; FAM 65577–65582, edentulous mandibles; FAM 65566, 65567, partial skulls; FAM 65586, two humeri.

Horizon and Locality.—Observation Quarry, "Sand Canyon beds," Dawes County, Nebraska.

Age.—Earliest Barstovian (middle Miocene).

Diagnosis.—Largest species of the genus; greater number of fossettes (-ids) on the premolars (P^4: $\bar{x} = 8.3$, mode 9; P_4: $\bar{x} = 8.4$, mode 8).

Etymology.—Patronym for T. Galusha.

Description.—The two skull fragments of this species preserve only the anterior half of the skull. Both show enlarged bony bosses at the end of the nasals, and are generally heavily built. The premaxillaries are laterally splayed at their dorsal extent to accommodate the enlargement of the anterior end of the nasals and development of the nasal bosses. The centers of these bosses are more anterior than the centers of the horn cores in even the most primitive species of *Ceratogaulus*. Due to breakage, little else can be determined about the skulls.

The premolars are generally larger than in other mylagaulids and are proportionally wider than in species of *Ceratogaulus* (ratio of width to length of P^4 approximately equals 0.75). The upper premolars (represented by only four specimens) are nearly circular in occlusal outline. The number of fossettes ranges from 7 to 9 with 9 as the modal number. The anterior branches of the parafossette do not separate on any of the available specimens, suggesting that any separation will occur in only very late stages of wear. There are several small, circular to oval fossettes along the buccal margin of the tooth posterior to the parafossette. The lingual fossettes are elongated.

The lower premolars are less circular in outline, being distinctly longer than wide but still relatively wider than in other mylagaulines. The number of fossettes ranges from 7 to 11 ($\bar{x} = 8.4$, mode = 8), more than in most other mylagaulines except the most advanced Hemphillian species of *Hesperogaulus* (Shotwell, 1958; Korth, 1999*a*). The fossettids are arranged anteroposteriorly in three rows—lingual, central, and buccal. The buccal row usually consists of only two elongated fossettids and the central row of three. The greatest variability occurs in the lingual row of fossettids. The number of fossettids in this row can range from two to as many as five. The size and shape of the fossettids in the lingual row are clearly dependent on the number. If the fossettids are small and circular, there can be many of them, if elongated, there are fewer fossettids. On approximately 50% of the specimens of P_4, the anterocentral fossettid is anteriorly forked or widened. In some cases a minute fossettid is in the place of one of the branches of the fork.

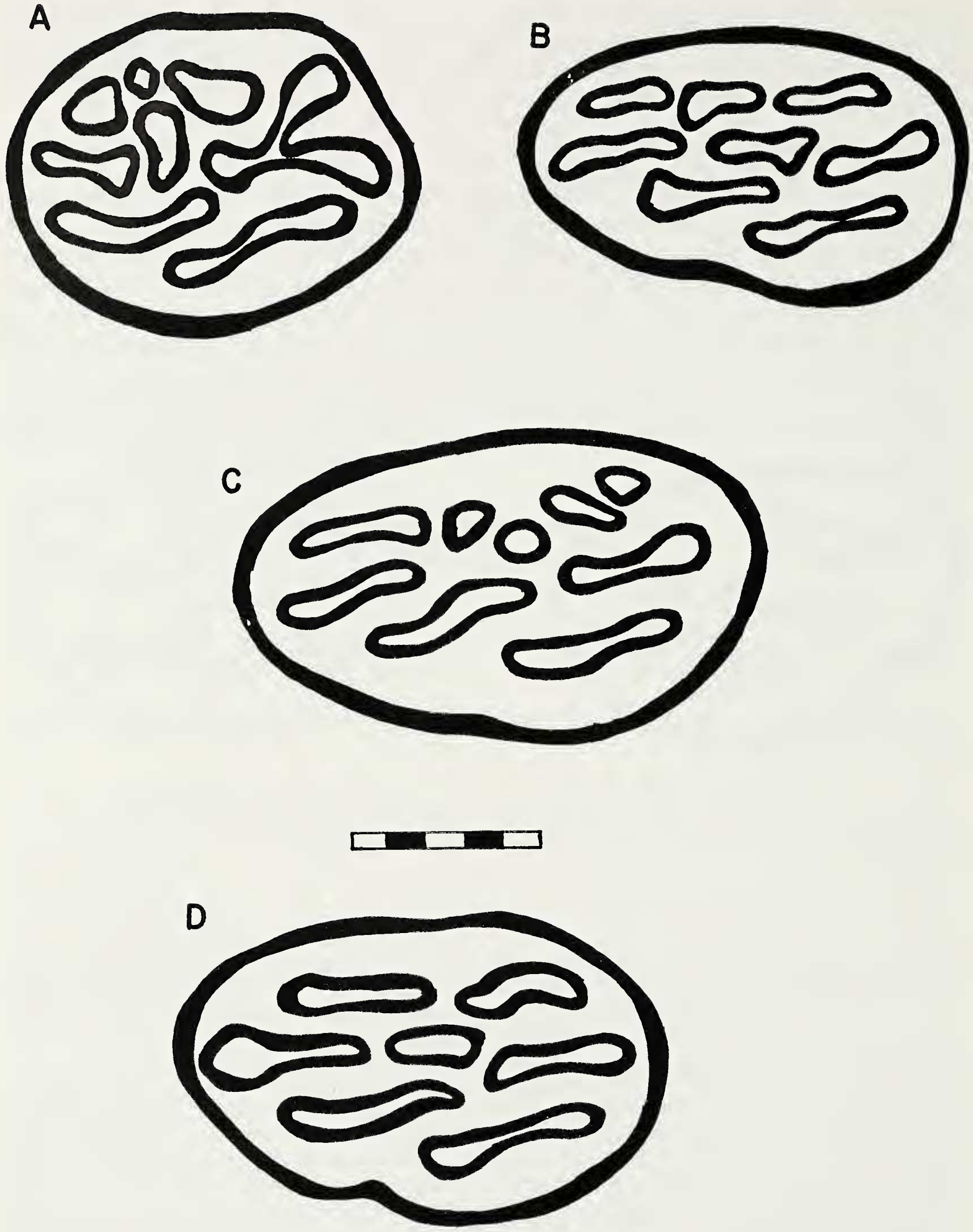

Fig. 10.—Premolars of *Umbogaulus galushai*. A. FAM 65568, right P^4. B. FAM 65574, left P_4. C. FAM 65575, left P_4. D. FAM 65576, holotype, left P_4. Bar scale = 5 mm.

Discussion.—Although the morphology of the nasal bosses and their position on the skull of *Umbogaulus galushai* appear to be primitive relative to species of *Ceratogaulus*, the size and complexity of the cheek teeth exceed that of any species of the latter, so it is unlikely that *U. galushai* is the ancestor to any species of *Ceratogaulus* even though the temporal occurrence (earliest Barstovian) is appropriate for an ancestor of *Ceratogaulus.*

Among all species of mylagaulids, *Umbogaulus galushai* most closely resembles the holotype of "*Mylagaulus*" *mondon* (AMNH 8327). The latter is slightly smaller than *U. galushai* with fewer fossettids on P$_4$. "*M.*" *monodon* cannot be referred to the same species as *U. galushai,* but is referable to the same genus.

Umbogaulus monodon (Cope, 1881*a*)
(Fig. 11B, 12; Table 5)

Mylagaulus monodon Cope, 1881*a.*

Type Specimen.—AMNH 8327, partial mandible with incisor and P$_4$.

Referred Specimens.—AMNH 13866, 13868, 13869,17215, 18899, 21466, 22044, 22045, 81071, 81074, 81077, 81080, 81081, 81084, 81085, 81592, 95047, 95054, 95056, 95057; FAM 65713–65716, 65785, 65944, isolated premolars; FAM 65695, mandible with cheek teeth; FAM 65016, 65712, 65784, partial skulls.

Horizon and Locality.—Holotype from Ogallala Group, Driftwood Creek (Hazard Homestead quarry), Hitchcock County, Nebraska; all referred specimens from various localities in the Olcott Formation, Sioux County, Nebraska.

Age.—Early and late Barstovian.

Diagnosis.—Slightly smaller than *U. galushai*; fewer fossettes on the premolars (P^4: $\bar{x} = 7.9$, mode 8; P$_4$: $\bar{x} = 7.3$, mode 7).

Description.—The nearly complete skull of this species lacks only the nasal bones. It is evident that it is a robust skull, similar to that of *U. galushai* and is posteriorly widened (W/L = 0.87). The only evidence for the formation of large bosses on the anterior end of the nasals is the splaying of the premaxillaries along the naso-premaxillary suture. This morphology is present in the skulls of *U. galushai* that preserve the nasals. The postorbital processes are intermediate in size, probably reflecting the primitive conditon in mylagaulids (POI = 0.35). The occipital is slightly tilted anteriorly (OA = 75°) but not as much as in most other advanced mylagaulines. In all other features, the skull of *U. monodon* is like the cranial material of all other mylagaulines.

The premolars, as in the type species of the genus, are larger and relatively wider than in other mylagaulines. The parafossette of P^4 remains forked until late stages of wear, when either of the branches may be separate. The number of fossettes varies from six in a very young individual to as many as ten. Both the mean and modal number of fossettes are fewer than in *U. galushai* ($\bar{x} = 7.9$, mode 8).

The lower premolars are very similar to those of the type species, differing only in being slightly smaller (Table 5) and having slightly fewer fossettids ($\bar{x} = 7.3$, mode = 7). The anterocentral fossettid of P$_4$ is also forked or widened as in *U. galushai.* This occurs in approximately 65% of the specimens, a higher percent than in *U. galushai.*

Discussion.—*Mylagaulus monodon* was the second species of the genus described by Cope (1881*a*). It was from the Republican River beds, Hitchcock County, Nebraska. This species was based on a single mandible with an incisor and P$_4$ (AMNH 8327). The locality from which this specimen was collected has been determined to be late Barstovian in age (Fiorillo, 1988; Voorhies, 1990*a*).

Nearly all specimens of large mylagaulids from the Barstovian to the Hemphillian that have not been associated with cranial material, as well as some hornless skulls, have been referred to *Mylagaulus monodon* (Wilson, 1937*a*, 1937*b*; McGrew, 1941; Gregory, 1942; Webb, 1969; Baskin, 1979; Korth, 1998). In spite of this universal use of the species name, the holotype of *M. monodon* does not appear to match any of this referred material. Even though more collections have been made at the type locality of this species (Fiorillo, 1988), no topotypic material has been found to define better the species itself. The holotype

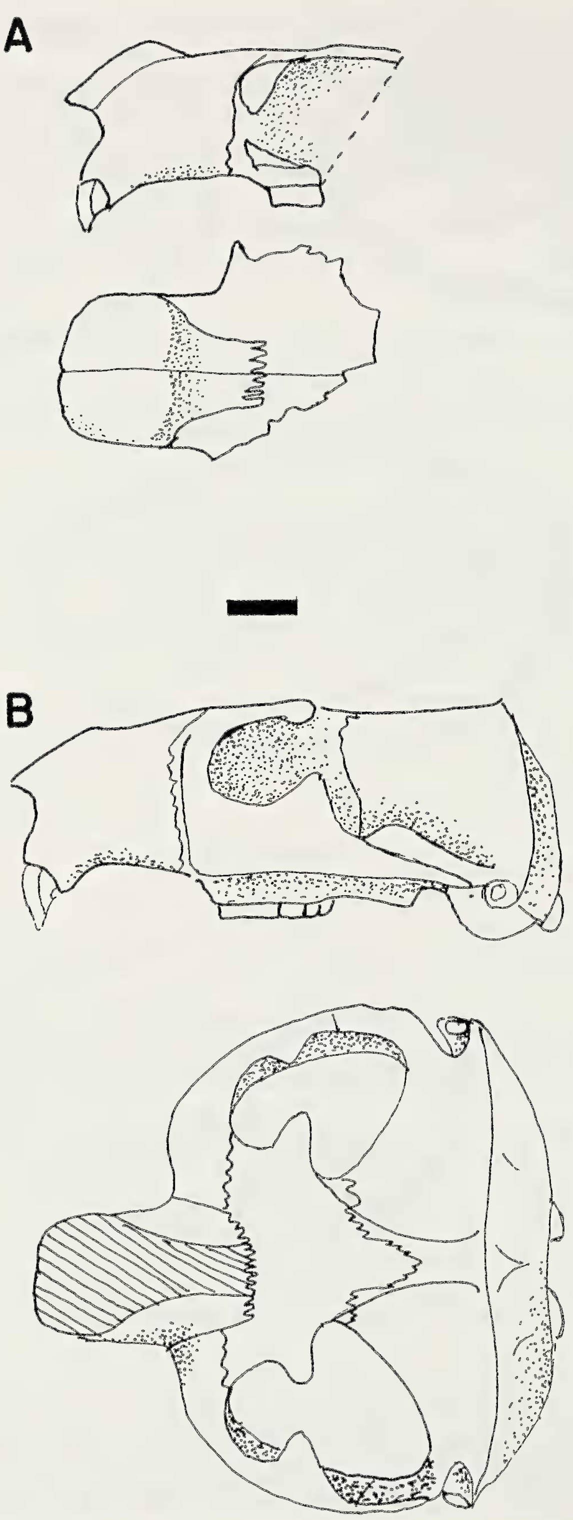
A
B

Table 5.—*Measurements of premolars of* Umbogaulus. *Statistical abbreviations as in Table 4.*

		n	x̄	OR	*s*	*cv*
Umbogaulus galushai						
P^4	a–p	4	10.88	10.20–12.00	0.68	6.28
	tr	4	7.21	6.40–7.65	0.48	6.73
P_4	a–p	21	12.02	10.30–13.25	0.79	6.56
	tr	22	6.53	5.50–7.55	0.58	8.81
Umbogaulus sp., cf. *U. monodon*						
P^4	a–p	28	10.24	8.50–12.30	0.97	9.40
	tr	27	6.26	5.50–7.60	0.46	7.28
P_4	a–p	32	11.05	4.50–13.15	1.00	9.06
	tr	32	5.54	4.75–7.10	0.55	9.84

of *M. monodon* differs from the species of *Mylagaulus*, which are characterized by having smaller, more simplified lower premolars (fewer fossettids). The type premolar of *M. monodon* is much larger with more fossettids. It is clear that "*M.*" *monodon* cannot be referred to *Mylagaulus*.

All of the referred specimens of *Umbogaulus monodon* listed above are from the early Barstovian Olcott Formation. There is no morphological difference between this sample and the holotype of the species, but there is a distinct age difference between the holotype (late Barstovian) and the referred material (early Barstovian).

Among known species of mylagaulids, the lower premolars of *Umbogaulus galushai* most closely resemble the type specimen of *M. monodon*, therefore the latter is referred to *Umbogaulus*. The lower premolars of *U. galushai* are distinct from those of *U. monodon* in being slightly larger and having more fossettids.

Mylagaulus Cope, 1878

Type Species.—*Mylagaulus sesquipedalis* Cope, 1878.

Included Species.—*Mylagaulus kinseyi* Webb, 1966, and *M. elassos* Baskin, 1980.

Range.—Possibly late Barstovian of Kansas and Nebraska; Clarendonian and Hemphillian of Florida.

Emended Diagnosis.—P^4 with posterobuccal fossette C-shaped (open posterobuccally) and parafossette with lingual branch separated first in early wear (as in *Ceratogaulus*); P^4 oval in occlusal outline (no indication of stylar cusps); P_4 simpler, with fewer fossettids (six) than other advanced mylagaulines.

Discussion.—Baskin (1980) demonstrated that the two species of *Mylagaulus* from the Clarendonian and Hemphillian of Florida, *M. kinseyi* and *M. elassos*, belonged to a lineage that reduced size through time. The only species of *Mylagualus* from the Great Plains with smaller size was the type species, *M. sesquipedalis*. The separation of the lingual branch of the parafossette of P^4, generally smaller size, reduced complexity (fewer fossettes [-ids] on the premolars), and

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←

Fig. 11.—Skulls of *Umbogaulus*. In both A and B top is left lateral view, bottom is dorsal view. A. *Umbogaulus galushai*, FAM 65566. B. *Umbogaulus monodon*, FAM 65016. Nasals missing on B. Bar scale = 1 cm.

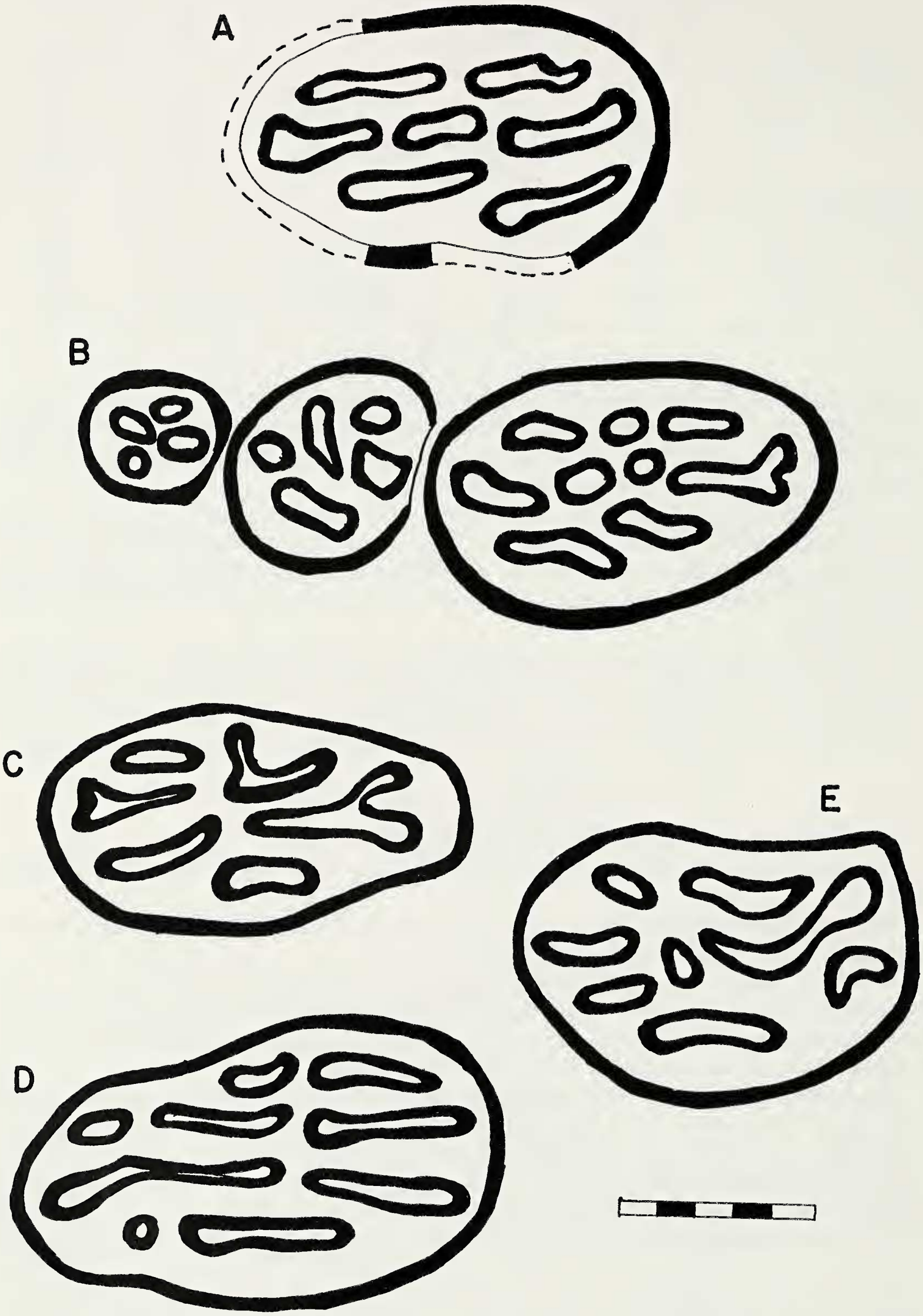

Fig. 12.—Premolars of *Umbogaulus monodon*. A. AMNH 8327, holotype, left P_4. B. FAM 65695, right P_4, M_2–M_3. C. FAM 95057, right P^4. D. AMNH 22044F, right P^4. E. FAM 95052, left P^4. Bar scale = 5 mm.

the C-shaped posterobuccal fossette on P^4 are features that are shared by *M. sesquipedalis* and the Florida species, making these three species a distinctive genus.

The only significant difference between *M. sesquipedalis* and the Florida species is its larger size. The temporal occurrence of *M. sesquipedalis*, possibly latest Barstovian (see discussion below), fits well into the sequence of species of *Mylagaulus* from larger to smaller through time. Being the earliest species, *M. sesquipedalis* is the largest species, *Mylagaulus elassos* from the Clarendonian is slightly smaller, and *M. kinseyi* from the late Hemphillian is the smallest species (see Baskin, 1980:fig. 1).

Mylagaulus sesquipedalis Cope, 1878
(Fig. 13)

Type Specimen.—AMNH 8329, left P^4.

Possible Referred Specimen.—AMNH 8330, left P_4.

Horizon and Locality.—Holotype from Ogallala Group, Sappa Creek, Rawlins County, Kansas. Referred specimen from the "Republican River Beds," Driftwood Creek, Hitchcock County, Nebraska.

Age.—?Late Barstovian.

Emended Diagnosis.—Largest species of the genus.

Discussion.—Cope (1878) erected *Mylagaulus sesquipedalis* based on an isolated upper premolar. The age of the fauna from Sappa Creek, from which the holotype of *M. sesquipedalis* came, is uncertain but has been referred to by previous authors as Clarendonian (Hibbard and Phillis, 1945:552; Baskin, 1980). However, it appears that the Sappa Creek fauna may be older than previously thought. The AMNH specimens from the Sappa Creek fauna include those collected by Cope's field parties in the late 1870s, and a few specimens collected by George Sternberg for the Frick Collections in the early 1930s. Besides the holotype of *Mylagaulus sesquipedalis*, the collected fauna consists of five mammalian taxa: a horse, *Protohippus medius*; a rhino, *Teleoceras fossiger*; a peccary, *Prosthennops servus*; a mastodont, *Tetralophodon campester*; and a merycodont artiodactyl, *Ramoceros kansanus*. *Protohippus medius*, *Prosthennops servus*, and *Tetralophodon compester* are represented by the holotypes of each of these species. The holotype of *P. medius* (AMNH 8360) is the skull of a senile individual where the teeth are completely worn, eliminating nearly all of the occlusal pattern. This species of *Protohippus* has not been recognized by any later workers (notably Osborn, 1918; and Stirton, 1940). The specimen has facial fossae consistent with those of *Protohippus*, and a size equivalent to that of *P. perditus* (R. L. Evander, personal communication) which is limited to the late Barstovian of Nebraska (Voorhies, 1990*a*). The merycodont similarly limits the age of the fauna because *Ramoceras* does not extend any later than the late Barstovian in the Nebraska section (Voorhies, 1990*a*). However, the peccary is very large and is similar to Hemphillian species. There is clearly a mixing of faunas in the Sappa Creek fauna. The mastodont is an advanced species which suggests a younger, possibly Hemphillian age. The rhino is known elsewhere to be late Clarendonian or early Hemphillian in age. Clearly, further collecting in the type area of Sappa Creek is necessary to verify the age of the fauna.

Matthew (1902) reported on a second specimen of *M. sesquipedalis*, AMNH 8330, that included a lower premolar, an incisor, and a metacarpal. He stated that

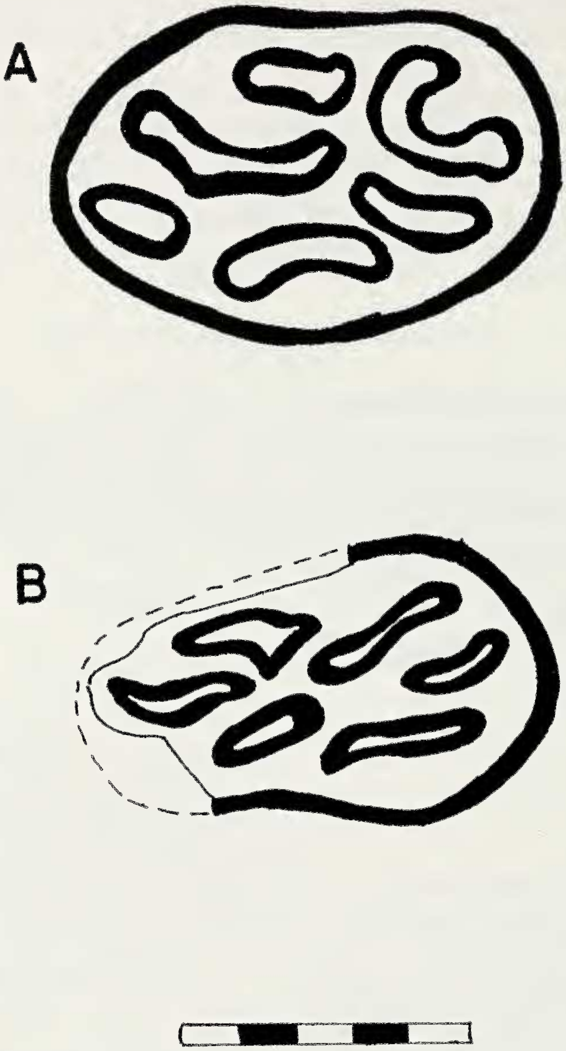

Fig. 13.—Dentition of *Mylagaulus sesquipedalis*. A. holotype, AMNH 8329, right P^4. B. paratype, AMNH 8330, left P_4. Bar scale = 5 mm.

the referred specimen was from the same locality as the holotype of *M. monodon*, Driftwood Creek, which is late Barstovian in age (Fiorillo, 1988; Voorhies, 1990*a*). At present, only the holotype and referred premolar are in the AMNH collections. The isolated incisor and metacarpal of the referred specimen cannot be located. While the reference of the referred P_4 to *M. sesquipedalis* may be questionable, it is morphologically consistent with the remainder of the species referred to the genus, *M. kinseyi* and *M. elassos*. This specimen was previously figured by Cope and Matthew (1915:pl. CXIXc, fig. 10), but was mistakenly labelled as the holotype. The occurrence of the referred specimen from a late Barstovian indicates that the species occurred at this time.

Both Hibbard and Phillis (1945) and Korth (1998) discussed the possibility of the synonymy of the Clarendonian species *Epigaulus minor* and *M. sesquipedalis*, noting that no conclusion could be drawn simply because of the lack of comparative material. The upper premolars of *E. minor* are slightly larger than the holotype of *M. sesquipedalis* and they are also wider relative to length. The morphology of the parafossette on P^4 is the same on both species, but the morphology of the posterobuccal fossette on specimens of *E. minor* is not the rounded C-shape that is diagnostic of *M. sesquipedalis*. If, however, these species do prove to be synonymous in the future, *Mylagaulus* would have priority, making the presence of horns on the nasals a generic character for *Mylagaulus*.

Ceratogaulus Matthew, 1902

Type Species.—*Ceratogaulus rhinocerus* Matthew, 1902.

Diagnosis.—Large mylagaulines; horns present on nasal bones; postorbital processes progressively reduced (POI $\leq$ 0.20); slope of occipital in Hemphillian species not as low as in other genera (OA = 60°–63°); occipital crest forms straight, transverse line (not deflected anteriorly as in other genera); upper premolars relatively wide (width to length ratio $\geq$ 0.68); lingual branch of parafossette separates first on P^4; anterolingual fossette attaches to lingual branch of parafossette on P^4 with wear; anterocentral fossettid of P_4 V-shaped in early wear.

Included Species.—*Ceratogaulus hatcheri* (Gidley, 1907), *C. minor* (Hibbard and Phillis, 1945), and *C. anecdotus*, n. sp.

Range.—Early Barstovian to Hemphillian (middle to late Miocene) of the northern Great Plains.

Discussion.—*Ceratogaulus* differs from all other mylagaulids in the possession of horns (or horn cores) on the nasal bones. The progressive changes in the genus through time are the more posterior placement of the nasal horns and reduction of the postorbital processes (Fig. 14). The nasal horns not only are placed progressively more posteriorly on the skull, but the horns also have narrower bases and are generally taller. In the late Barstovian *C. rhinocerus*, the horns are pointed but have a very wide base, giving them a pyramid-like profile. In the Clarendonian specimens of the former, the nasals are slightly more posterior (NHI = 0.16–0.22). In the Hemphillian *C. hatcheri*, the horns have narrow bases, are circular in cross section, and are nearly dorsal to the orbits (NHI $\geq$ 0.28). Similary, the postorbital processes are reduced through time: in *C. rhinocerus* they are moderately large (POI = 0.18–0.26), probably near the primitive condition; in *Ceratogaulus* sp., cf. *Ceratogaulus rhinocerus* in the early Clarendonian, the processes are smaller (POI = 0.12–0.15); and, ultimately, in Hemphillian species the postorbital processes are nearly absent (POI = 0.11).

Gidley (1907) named *Epigaulus* for a species, *E. hatcheri*, from the Hemphillian of Kansas, noting that it differed from the type of *Ceratogaulus rhinocerus* (only known species of the genus at that time) from the Barstovian in the more posterior position of the nasal horns, more enlarged premolars, and presence of cement around the premolars. All of these characters are now known to represent gradational changes in the known species of *Ceratogaulus* from throughout the entire time of occurrence of the genus (Table 1). There is no evidence indicating that *Epigaulus* exists as a genus separate from *Ceratogaulus*, but more likely represents the most derived species.

Ceratogaulus is geographically restricted to the northern Great Plains from Kansas to Saskatchewan. Species of *Ceratogaulus* are frequently found in faunas

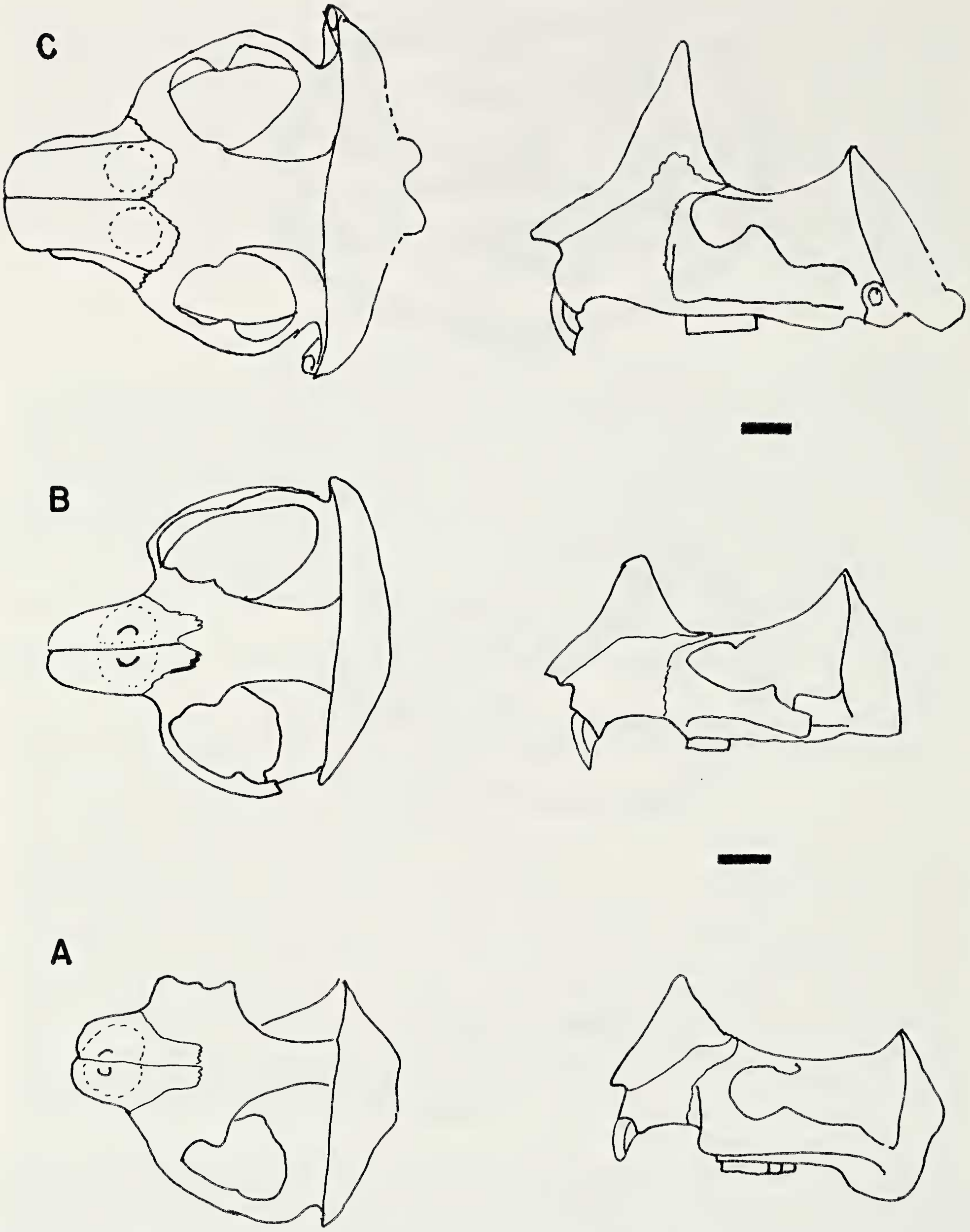

Fig. 14.—Outlines of skulls of *Ceratogaulus* showing progressive changes through time (position of nasal horns and reduction of postorbital process). Dorsal view on left, left lateral view on right. A. Barstovian *C. rhinocerus*, AMNH 9456 (holotype). B. Early Clarendonian *C.* sp., cf. *C. rhinocerus*, FAM 65385. C. Hemphillian *C. hatcheri* (holotype) USNM 5485. Bar scale = 1 cm.

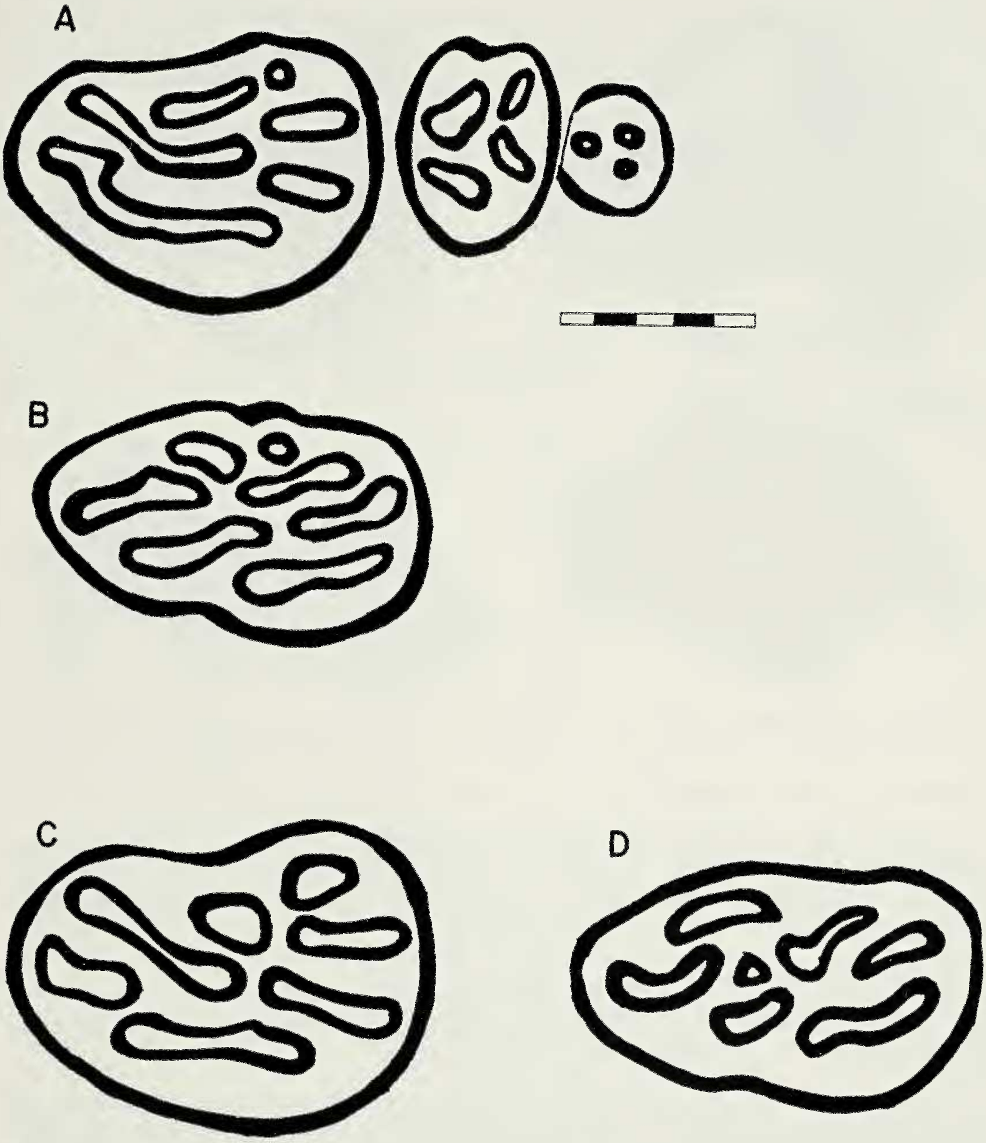

Fig. 15.—Premolars of *Ceratogaulus rhinocerus*. A, B. AMNH 9456 (holotype), Barstovian. A. Left P^4, M^2–M^3. B. Left P_4. C, D. *Ceratogaulus* sp., cf. *C. rhinocerus*, early Clarendonian (Burge). C. FAM 65385, left P^4. D. FAM 65408, left P_4. Bar scale = 5 mm.

that also contain species of a hornless genus of mylagauline described below (see discussion of *Pterogaulus*).

Ceratogaulus rhinocerus Matthew, 1902
(Fig. 14C, 15A, B; Table 6)

Type Specimen.—AMNH 9456, nearly complete skull with associated lower jaw (Matthew, 1902:fig. 1).

Table 6.—*Measurements of premolars of* Ceratogaulus. *Statistical abbreviations as in Table 4.*

		n	$\bar{x}$	OR	*s*	*cv*
Ceratogaulus rhinocerus						
Late Barstovian (Crookston Bridge Member)						
P^4	a–p	3	9.82	9.78–9.88	—	—
	tr	3	6.91	6.57–7.10	—	—
P_4	a–p	4	11.04	10.25–12.35	—	—
	tr	4	6.45	6.10–6.61	—	—
Late Barstovian (Devil's Gulch Member)						
P^4	a–p	3	9.50	8.30–11.60	—	—
	tr	3	6.70	5.70–8.40	—	—
P_4	a–p	1	9.20	—	—	—
	tr	2	5.75	5.70–5.80	—	—
Ceratogaulus sp., cf. *C. rhinocerus*						
Early Clarendonian (Burge Member)						
P^4	a–p	15	9.16	8.35–9.80	0.53	5.79
	tr	16	6.21	5.40–7.00	0.56	8.99
P_4	a–p	20	10.23	8.70–11.45	0.79	7.73
	tr	21	5.43	4.90–6.15	0.38	7.00
Ceratogaulus anecdotus						
Late Clarendonian (Merritt Dam Member)						
P^4	a–p	3	10.16	9.10–12.20	—	—
	tr	3	6.86	6.20–7.90	—	—
P_4	a–p	3	12.66	10.00–14.70	—	—
	tr	4	5.55	5.05–6.70	—	—

Referred Specimens.—AMNH 18899; UNSM 122005, 122007, 122010, 122009.

Horizon and Locality.—Holotype from Pawnee Creek beds, Logan County, Colorado; AMNH 18899, from Olcott Formation, Sioux County, Nebraska; UNSM specimens from Crookston Bridge Quarry, Crookston Bridge Member, Valentine Formation, Cherry County, Nebraska.

Age.—Early to late Barstovian (middle Micoene).

Emended Diagnosis.—Horns on nasals positioned more anteriorly than in other species (NHI = 0.19–0.21), and not as tall; postorbital processes small, triangular flanges (POI = 0.19), larger than in other species.

Decription.—Matthew (1902) fully described and figured the skull of *Ceratogaulus rhinocerus.* The upper premolar has from five to ten fossettes ($\bar{x}$ = 7.4; mode = 7). While the mean number of fossettes on P^4 is slightly higher than other species of the genus, the modal number is identical for all species of *Ceratogaulus* (Table 2). The parafossette is the longest of the fossettes and its lingual branch separates from the rest of the fossette in early stages of wear. A single lingual fossette runs most of the length of the tooth, occasionally uniting anteriorly with the lingual branch of the parafossette once it has separated. The remainder of the fossettes on P^4 are smaller and directed anteroposteriorly. Frequently, there is one minute, circular fossette present along the buccal edge of the tooth just posterior to the center of the tooth. P^4 is not perfectly oval in occlusal outline. There is always a slight concavity along the buccal edge of the tooth (created by a vestige of the mesostyle) with its deepest curvature near the middle of the tooth.

The lower premolar has seven to ten fossettids ($\bar{x}$ = 7.7; mode = 7). There are three elongated fossettids along the lingual side and three along the buccal side of the tooth with one or more small, circular accessory fossettids randomly positioned. The elongated fossettids are all oriented obliquely (posterolingual to anterobuccal). The most anterior fossettid is V-shaped in early stages of wear with the apex of the V pointed posteriorly. After a moderate amount of wear, the lingual arm of the V separates from the rest of the fossettid, and ultimately disappears with additional wear.

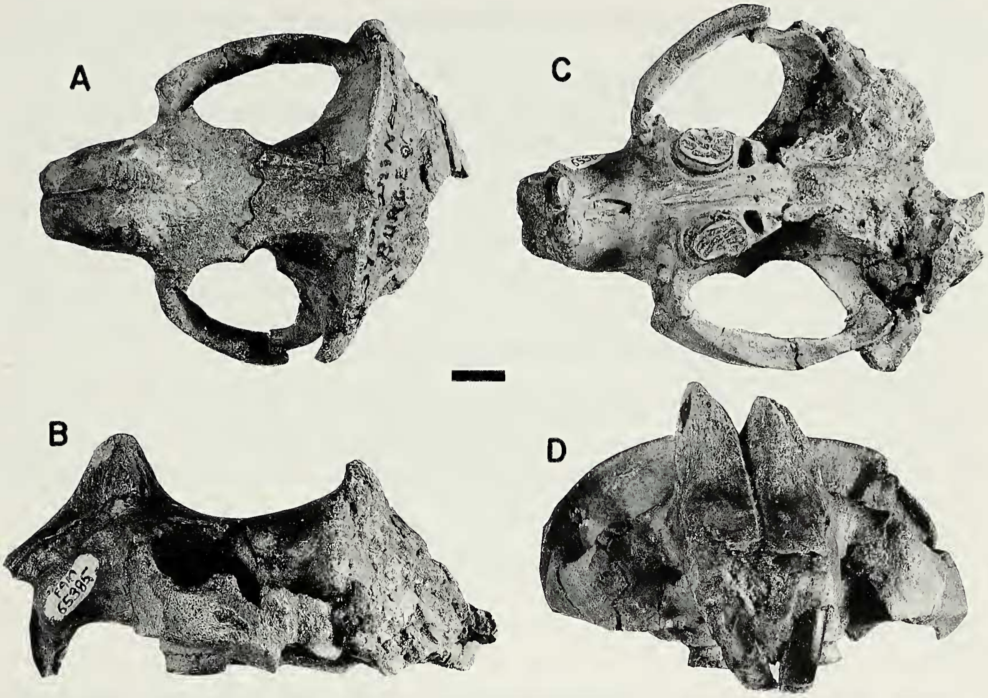

Fig. 16.—Skull of *Ceratogaulus* sp., cf. *C. rhinocerus*, FAM 65385, from Burge Quarry (early Clarendonian). A. Dorsal view. B. Left lateral view. C. Ventral view. D. Anterior view. Bar scale = 1 cm.

Discussion.—Specimens of *C. rhinocerus* show a consistent morphology of the skull and dentition throughout the entire range of the species. The dentition is especially conservative in terms of morphological change. There is little or no change in the size or morphology of the premolars from the early Barstovian to the early Clarendonian.

Ceratogaulus rhinocerus differs from the late Clarendonian and Hemphillian species of *Ceratogaulus* mainly in the morphology of the premolars. The upper premolars of *Ceratogaulus* are relatively wide compared to their length (length to width ratio of ≥ 0.71). P^4 of *C. rhinocerus* is not entirely oval in outline, maintaining a slight concavity on the buccal margin between the mesostyle and parastyle. Later species of *Ceratogaulus* have much narrower premolars (P^4 length to width ratio ≤ 0.65), cement appears around the premolars at an earlier stage of wear, and the premolars are oval in outline, lacking the slight buccal concavity present on P^4 of *C. rhinocerus*.

Ceratogaulus sp., cf. *C. rhinocerus*
(Fig. 14B, 15C, D, 16; Table 6)

Referred Specimens.—FAM 65012, 65013, 65370, 65371, 65373, 65374, 65375, 65377, 65385, 65388, 65398, 65399, 65403, 65404, 65406, 65408, 65412, 65413, 65418, 65420, 65422, 65476, 65489, 65833; UNSM 122006.

Horizon and Locality.—All specimens from various quarries (Burge, Midway, White Face, Lucht, June, Gordon Creek) in the Burge Member, Valentine Formation, northcentral Nebraska (see Skinner and Johnson, 1984, for location of quarries).

Age.—Early Clarendonian.

Discussion.—Dentally, it is virtually impossible to distinguish the Burge specimens of *Ceratogaulus rhinocerus* from those from lower in the Valentine Formation. However, the cranial material is somewhat different. The Burge specimens, referred here to *Ceratogaulus* sp., cf. *C. rhinocerus*, have more posteriorly placed horns and more reduced postorbital processes (Table 1). The skulls are also slightly larger. The slightly larger skull size is not reflected in the dimensions of the dentition (Table 6) or the complexity of the premolars (Table 2). The horns on the specimens from the Burge have narrower bases and are more nearly circular in cross section than those from the late Barstovian.

It would be impractical to name a new species for the Burge specimens at this time because the majority of the specimens recovered are dentitions which cannot be separated from the Barstovian specimens morphologically. The Burge skulls are clearly more advanced in having more posteriorly placed horns and smaller postorbital processes (Fig. 14, 16).

Ceratogaulus anecdotus, **new species**

(Fig. 17; Table 6)

Epigaulus minor Hibbard and Phillis; Korth, 1997 (in part).
Mylagaulus sp., cf. *M. monodon* Cope; Korth, 1997 (in part).

Type Specimen.—FAM 65800, fragmentary skull with both upper premolars and some postcranial fragments.

Referred Specimens.—FAM 65466, partial skull; FAM 65456, 65464 isolated P^4s; FAM 65456, associated upper and lower premolars; FAM 65430, 65468, 65481, 65497; UNSM 101813, mandible with P_4, M_2–M_3.

Horizon and Locality.—Holotype and some referred specimens from Pratt Quarry (UNSM locality Bw-123), Merritt Dam Member, Ash Hollow Formation, Brown County, Nebraska; other referred specimens from various localities in the Merritt Dam Member; FAM 65466 from "Prospect 28-18," Cap Rock Member, Ash Hollow Formation, Brown County, Nebraska.

Age.—Middle to late Clarendonian (early late Miocene).

Diagnosis.—Smaller than *C. hatcheri*, larger than other species of the genus; premolars more elongated than in *Ceratogaulus rhinocerus*, but less than in *C. hatcheri* (width to length ratio of P^4 = 0.64–0.66); fewer fossesttes (-ids) on premolars than in *C. hatcheri*; P^4 oval in occlusal outline; cement surounds premolars in an earlier stage of wear than in *C. rhinocerus*; postorbital process subequal to that of *C. hatcheri* and smaller than in *C. rhinocerus* (POI = 0.12); nasal horn less posterior than *C. hatcheri*, more posterior than in *C. rhinocerus* (NHI = 0.30).

Etymology.—Greek, *anekdotos*, unpublished or secret.

Description.—The nearly complete skull of a juvenile individual of *C. anecdotus*, FAM 65466, is badly broken but most of the morphology of the skull is recognizable. A nearly complete skull in the UNSM collections (field number 2-26-5-15) is being studied elsewhere, but allows for a determination

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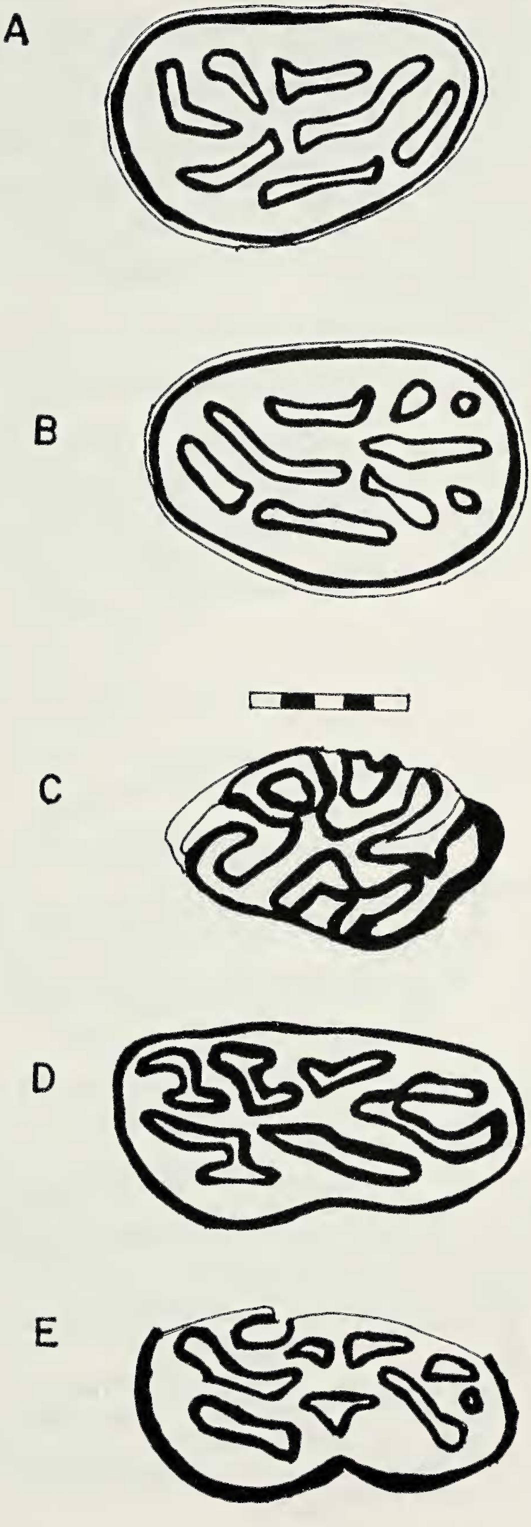
Fig. 17.—Dentition of *Ceratogaulus anecdotus*. A, B. Holotype, FAM 65800. A. Right P^4. B. Left P^4. C. FAM 65484, right P_4. D. UNSM 101813, right P_4. E. FAM 65497, right P_4. Bar scale = 5 mm.


A
B
C
D
E

of the position of the nasal horn (NHI = 0.30) and the angle of the occipital (OA = 60°). The holotype also contains fragments of the skull including a complete nasal bone that preserves the horn. The horn is roughly circular in cross section and is posteriorly positioned. Its position is slightly more anterior than in *C.hatcheri* but more posterior than in any skull of *Ceratogaulus rhinocerus* (Table 1). The postorbital processes are more reduced than in any other species of *Ceratogaulus* except *C. hatcheri*. The premolars are larger than those of *C. rhinocerus*, but smaller than those of *C. hatcheri*. The number of fossettes on P^4 ranges from 6 to 9, similar to that of *C. rhinocerus* (Table 2). P^4 is narrower than in *C. rhinocerus* and *C. minor* (width to length ratio = 0.65). One specimen of P^4 (FAM 65465) has little wear and appears a little wider, within the range of *C. rhinocerus*. The arrangement of the fossettes of P^4 is similar to those of *C. minor* and *C. rhinocerus*, differing only in having several minute fossettes on the posterior half of the tooth. The two P^4s of the holotype are only moderately worn and already are completely surrounded by cement. This appears to occur much earlier in *C. anecdotus* than in *C. rhinocerus*.

The lower premolars of *C. anecdotus* differ from those of *C. rhinocerus* in the same way as do the upper premolars. The range of the number of fossettids is 6 to 10, again similar to the range in *C. rhinocerus*. The only other differences between P_4 of *C. anecdotus* and those of *C. rhinocerus* are larger size and earlier appearance of cement around the tooth.

Discussion.—*Ceratogaulus anecdotus* is more advanced than *C. rhinocerus* based on the morphology of the horn (more posterior, circular cross section), proportions of the premolar, reduction of the postorbital process, larger size, and earlier occurrence of cement around the cheek teeth. It differs from *C. hatcheri* in having a more anteriorly placed horn, smaller size, and fewer fossettes (-ids) on the premolars.

Korth (1997) originally referred the holotype of *C. anecdotus* to *Epigaulus minor*. However, this specimen differs from *C. minor* not only in the cranial features cited above, but also in its larger size and narrower upper premolars. Similarly, a specimen figured by Korth (1997:fig. 1B) as *Mylagaulus* sp., cf. *M. monodon*, UNSM 101813, is clearly referable to *C. anecdotus* with the characteristic V-shaped anterior fossettid on P_4.

Pterogaulus, new genus

Type Species.—Mylagaulus laevis Matthew, 1902.

Referred Species.—*P. cambridgensis* (Korth, 2000), *P. barbarellae* n. sp., and *Pterogaulus* sp.

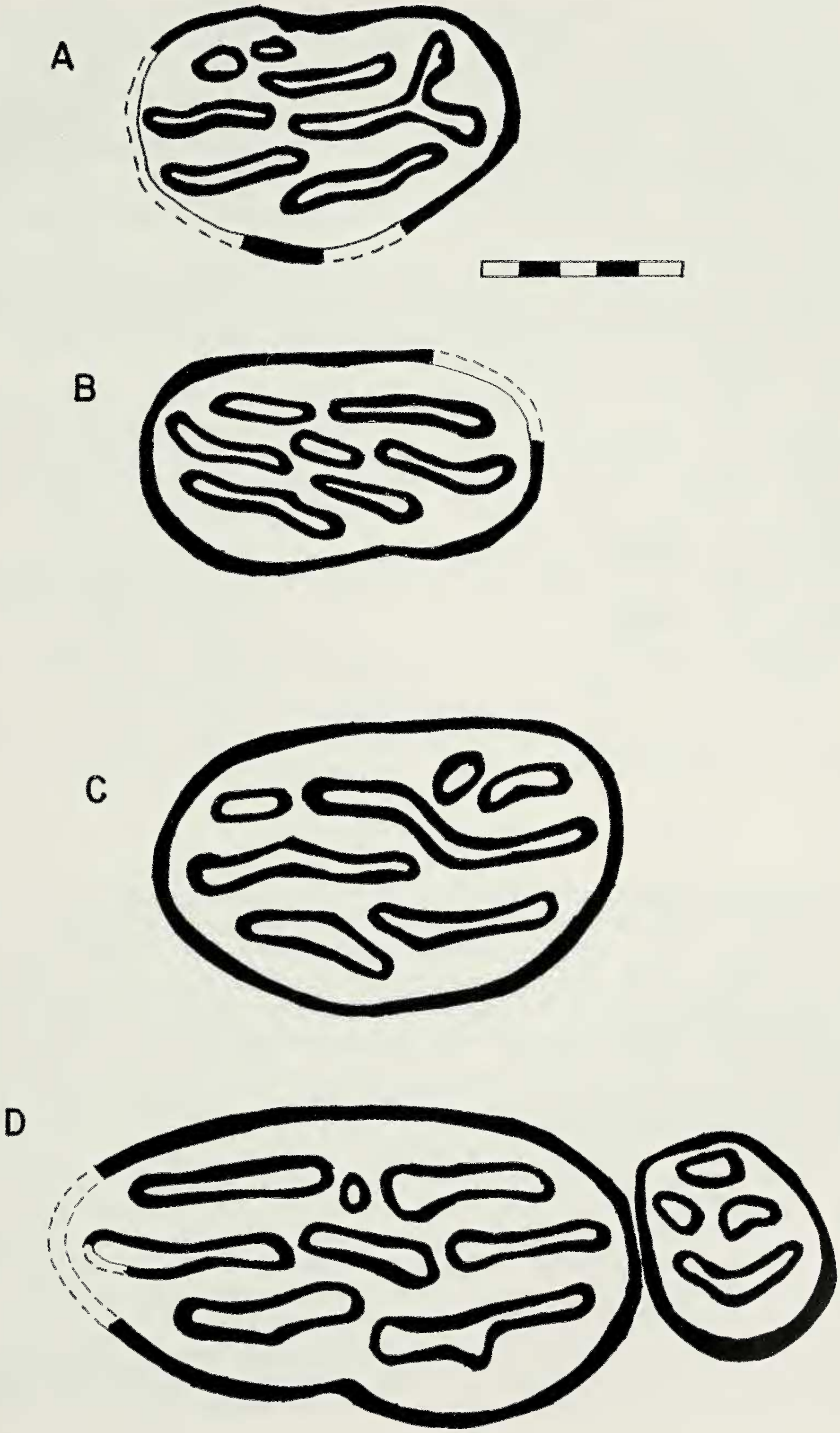
Range.—Barstovian to Hemphillian of northern Great Plains.

Etymology.—Greek, *pteron*, wing; and *gaulos*, bucket.

Diagnosis.—Intermediate to large mylagaulines; horns or bosses lacking on nasals; frontals with enlarged, wing-like postorbital processes (POI = 0.39–0.57); angle of occipital in advanced species generally lower than in other genera (OA < 60°) but not as low as in *Hesperogaulus*; occlusal pattern of premolars with anteroposteriorly oriented linear fossettes(-ids); in advanced species, first and second molars lost with eruption of permanent premolars; buccal branch of parafossette on P^4 separates from remainder of fossette first; premolars more anteroposteriorly elongated than in *Ceratogaulus* (P^4 width to length ratio ≤ 0.68).

→

Fig. 18.—Premolars of *Pterogaulus laevis* and *P. barbarellae*. A, B. *Pterogaulus laevis*, AMNH 9043, holotype. A. Right P^4. B. Right P_4. C, D. *Pterogaulus barbarellae*. C. FAM 65491, holotype, left P^4. D. FAM 65493, left P_4, M_2. Bar scale = 5 mm.


A
B
C
D

Pterogaulus laevis (Matthew, 1902)
(Fig. 18A, B, 19A; Table 7)

Mylagaulus monodon (in part) Matthew, 1901.
Mylagaulus laevis Matthew, 1902.

Type Specimen.—AMNH 9043, anterior half of skull with associated mandible and pelvis (Matthew, 1901:figs. 3, 4, 5, 6).

Referred Specimens.—KU 9807, 9808, 9969; and specimens from Sioux County, Nebraska cited in Matthew (1924:78).

Horizon and Locality.—Holotype and KU specimens from Pawnee Creek Formation of northeastern Colorado (Matthew, 1924), referred specimens from Olcott Formation, Sioux County, Nebraska (Matthew, 1924; Skinner et al., 1977).

Age.—Barstovian (middle Miocene).

Emended Diagnosis.—Smallest species of the genus; postorbital process smaller than in other species (POI = 0.39–0.41); angle of occipital greater than in late Barstovian and Clarendonian species (OA = 68°–75°); parafossette of P^4 more persistent than in other species (buccal branch separates very late in wear); fewer number of fossettes (-ids) on premolars than in later species (P^4: $\bar{x} = 6.5$, mode = 6; P_4: $\bar{x} = 5.7$, mode = 5).

Discussion.—Matthew (1901, 1902, 1924) fully described and figured the skull and dentition of *Pterogaulus laevis*. The skeleton was fully described by Fagan (1960).

This species is both temporally older and morphologically more primitive than later species of this genus. Its early Barstovian occurrence predates that of all other species. In its smaller size and morphology of the skull (angle of occipital, size of postorbital processes) and dentition (fewer fossettes, separation of parafossette fork later in wear), it is clearly more primitive than the later species.

Pterogaulus sp.
(Table 7)

Discussion.—Several authors have previously identified specimens of this species from the Barstovian of Nebraska and Saskatchewan as *Mylagaulus* cf. *M. laevis* (Storer, 1975; Voorhies, 1990*b*; Evander, 1999). The cranial and dental features of this species are clearly intermediate between those of the early Barstovian *Pterogaulus laevis* and the late Clarendonian species described below. This previously described material, and additional material more recently recovered by UNSM clearly represents a new species. However, the description and naming of this species will not be presented here; it is part of a larger faunal study currently underway by workers at UNSM.

The stratigraphic range of *Pterogaulus* sp. is similar to that of *Ceratogaulus rhinocerus*, but extends from the middle Barstovian to the middle Clarendonian, slightly later than the last occurrence of *C. rhinocerus* (early Clarendonian). There appears to be no discernible difference in morphology or size between specimens from the lowest level (Norden Bridge Quarry) and those from the highest level (Cap Rock Member), unlike specimens of *C. rhinocerus*, which show advancements in the skull in the early Clarendonian specimens.

While *Pterogaulus* sp. and *C. rhinocerus* are contemporaneous for most of their known records, they rarely occur at the same quarry. For example, at the Norden Bridge Quarry, West Valentine Quarry, and Stewart Quarry (see Voorhies, 1990*a*,

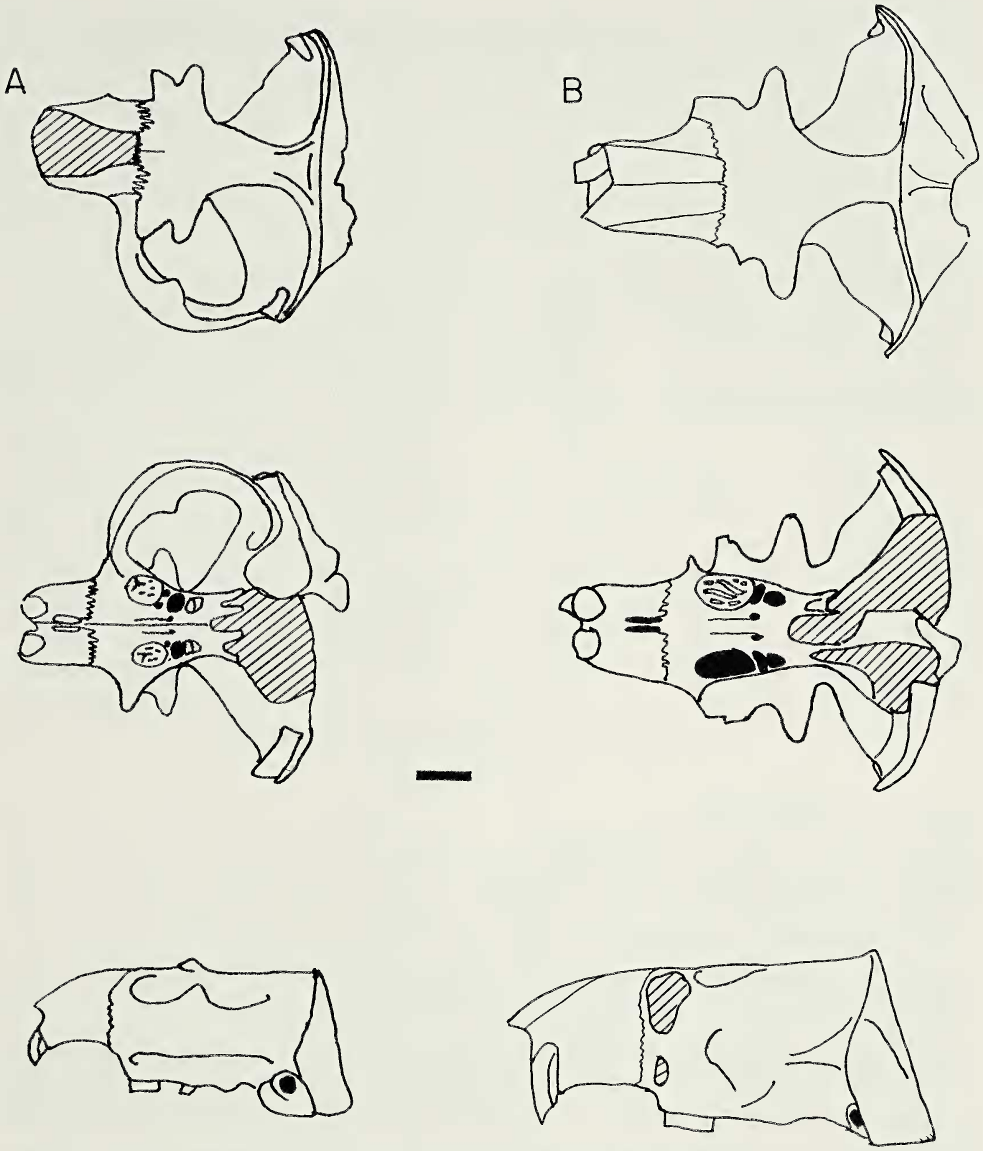


Fig. 19.—Skulls of *Pterogaulus*, dorsal view (top), ventral view (center), and left lateral view (bottom). A. *Pterogaulus laevis*, AMNH 17576. B. *Pterogaulus barbarellae* holotype, FAM 65491. Scale = 1 cm.

and Voorhies and Timperley, 1997, for location of quarries), where *Pterogaulus* sp. is abundant, there are no specimens of *Ceratogaulus*. In other quarries from the same horizon in the Valentine Formation, such as the Cornell Dam Quarry, only specimens of *C. rhinocerus* have been recovered. This suggests that these species were mutually exclusive in terms of geography, possibly competing for resources with one another.

Table 7.—*Measurements of premolars of* Pterogaulus. *Measurements from middle Barstovian sample of* Pterogaulus *sp. from Voorhies (1990*b*:A84). Statistical abbreviations as in Table 4.*

		n	$\bar{x}$	OR	*s*	*cv*
Pterogaulus laevis						
P^4	a–p	15	7.87	7.00–9.00	0.58	7.4
	tr	15	4.97	4.35–5.45	0.30	6.0
P_4	a–p	11	8.18	7.40–9.30	0.51	6.2
	tr	11	4.12	3.60–5.00	0.34	8.3
Pterogaulus sp. (middle Barstovian)						
P^4	a–p	8	9.0	8.3–10.0	—	—
	tr	8	5.5	4.8–6.5	—	—
P_4	a–p	9	9.4	8.7–10.2	—	—
	tr	9	5.0	4.5–5.5	—	—
Pterogaulus sp. (Clarendonian)						
P^4	a–p	9	8.9	7.6–10.2	0.8	8.9
	tr	9	5.8	5.4–6.4	0.3	5.2
P_4	a–p	2	9.8	8.5–11.2	—	—
	tr	2	5.0	4.75–5.2	—	—
Pterogaulus barbarellae						
P^4	a–p	19	10.48	8.80–12.50	1.20	11.48
	tr	18	6.27	5.55–7.50	0.62	9.91
P_4	a–p	18	11.40	9.45–13.30	1.19	10.41
	tr	18	5.43	4.85–6.85	0.51	9.36

Pterogaulus barbarellae, **new species**
(Fig. 18C, D, 19B; Table 7)

Mylagaulus ? Gregory, 1942.
Mylagaulus cf. *monodon* Webb, 1969 (in part).
Mylagaulus cf. *M. mondon* Voohries, 1990*a*.
Mylagaulus sp., cf. *M. mondon* Korth, 1997 (in part).
Mylagaulus monodon Cope, Korth, 1998 (in part).

Type Specimen.—FAM 65491, skull with P^4.

Referred Specimens.—FAM 65008, 65435, 65436, 65439–65443, 65446, 65448, 65454, 65465, 65475, 65491–65496, 65498, 65499, 65787, 65788, 65791, 65797.

Horizon and Locality.—Holotype from Xmas Quarry, Xmas and Kat Channels, Ash Hollow Formation, Cherry County, Nebraska; referred specimens from various late Clarendonian localities in Merritt Dam Member, Ash Hollow Formation, Nebraska.

Age.—Late Clarendonian (early-late Miocene).

Diagnosis.—Larger than *P. vetus* and *Pterogaulus* sp.; postorbital processes larger than in any other species (POI = 0.40–0.57); angle of occipital less than in other species (OA = 52°); fossettes(-ids) on premolars more elongated and anteroposteriorly aligned than in other species but similar in number (P^4: $\bar{x} = 7.8$, mode = 8; P_4: $\bar{x} = 6.5$, mode = 6); first two molars lost with eruption of permanent premolar.

Etymology.—Patronym for Barbara Lamb.

Description.—The skull of *Pterogaulus barbarellae* is more advanced than that of *Pterogaulus* sp. in having larger postorbital processes and having a lower angle of the occipital (Table 1). It is also clearly larger in size (Table 7). All other features of the skull appear to be the same as in all other species of the genus, with no indication of a horn or boss on the nasals.

The premolars of *P. barbarellae* are larger than in other species in proportion to the rest of the dentition. It appears that with the eruption of the permanent premolar, the first two molars are shed instead of just M^1 or M_1. P^4 has a nearly equal number of fossettes to P^4 of *Pterogaulus* sp. with a similar range (6 to 10) but a slightly greater mean number (7.8 rather than 7.2 for *Pterogaulus* sp.). The buccal fork of the parafossette is separated from the rest of the fossette on nearly all specimens. The only specimens that retain this connection are those of very young individuals with little or no wear on the teeth.

On P_4, the number of fossettids is not greater than in *Pterogaulus* sp. but they are relatively longer and more directly anteroposteriorly oriented, forming an almost linear pattern on the occlusal surface. The length of most of the main fossettids is approximately half the total length of the tooth.

Discussion.—Pterogaulus barbarellae is larger and more derived than either of the older species of the genus. It clearly follows the trends in morphology of the skull (larger postorbital processes, lower angle of occipital) and dentition (larger premolars, more elongated fossettes) that are recognizable in earlier species. Another species of this genus, *P. cambridgensis*, is present in the Hemphillian of Nebraska (Korth, 2000). The latter also follows these same morphoclines for the skull and dentition.

Ceratogaulus anecdotus is contemporaneous with *P. barbarellae*, similar to the case of *C. rhinocerus* and *Pterogaulus* sp. in the Barstovian and early Clarendonian. However, the occurrence of the late Clarendonian species does not appear to be mutually exclusive as is the case with the Barstovian species. In at least two localities (Beaman Creek, Pratt Quarry) specimens of both *C. anecdotus* and *P. barbarellae* are present. However, the fossil quarries in the late Clarendonian "Xmas and Kat Channels" (Skinner and Johnson, 1984) have produced only specimens of *Pterogaulus*. There are no specimens of *Ceratogaulus* in the AMNH Frick Collections from these quarries, although they were extensively collected.

CONCLUSIONS

Variation in Premolars within Species.—Black and Wood (1956) made a detailed study of the progressive changes in the number and shape of fossettes on the cheek teeth of the Hemingfordian "*Mesogaulus*" *novellus*. Shotwell (1958) sectioned the premolars of a number of specimens of later Tertiary mylagaulids to demonstrate ontogenetic changes in the species he discussed. Korth (1997) also discussed ontogenetic changes in premolars from the late Clarendonian specimens that he referred to *Mesogaulus monodon* (referred here to *Pterogaulus barbarellae*). The pattern of change in the occlusal morphology of premolars of mylagaulines in an individual, and the range of variation in a population, appear to be fairly consistent throughout the family.

The number of fossettes in a single premolar of any species varies throughout the life of the individual. In unworn specimens of premolars that are just reaching the level of occlusion, the number of fossettes is the fewest. At this time the major fossettes are often joined at their ends, forming a number of star-like fossettes with many branches. As the tooth reaches an intermediate stage of wear, the major fossettes separate from one another, and the highest number of fossettes is attained. In most senile individuals with heavily worn premolars, the number is near the maximum, with only a few of the smallest fossettes, which are shallower, being lost. At this time the proportions of the tooth are such that the tooth is much narrower than at any other time, and the fossettes(-ids) are generally more anteroposteriorly aligned and closely packed together.

Because the premolar tapers toward its base, once the tooth has worn past its maximum dimensions it becomes surrounded by a layer of cement. In *Mesogaulus* and primitive mylagaulines, this occurs in very late stages of wear. In the more advanced species, where the premolar is proportionally much larger, cement is present at the occlusal surface at an earlier stage of wear.

The parafossette of P^4 also shows some changes through the life of an individual. Originally, the parafossette maintains its two anterior branches. In more primitive species, these remain attached to the remainder of the fossette until very late stages of wear. When there is a preferred pattern of separation of the anterior forks of the parafossette, as in *Pterogaulus* or *Ceratogaulus*, this separation occurs at progressively earlier stages of wear (Fig. 20). Ultimately, in most specimens that are at extremely late stages of wear, both forks are separated from the main part of the parafossette and are minute, circular fossettes.

The greatest source of variation in the number of fossettes(-ids) on the premolars of a single sample of a mylagaulid species is the division of one of the major (longer) fossettes into two or more smaller fossettes. It is not uncommon to have specimens that have divided even two of these major fossettes into more, smaller fossettes. In looking at the range of variation in number of fossettes in a single sample, it appears that the calculation of the mean and modal number of fossettes is very useful. In some genera, such as *Umbogaulus*, there is a distinct progressive change over time in the number of fossettes among its species. The minimum number of fossettes also appears to be consistent within a single species. If the maximum number of fossettes is dependent on the division of the "major" fossettes, the minimum number will be little changed within a single sample.

Variation in Premolars among Species.—There is a general trend in mylagaulids, from the early, more primitive species to the latest, most specialized species: the number of fossettes(-ids) on the premolars increases. However, within any single genus, the number appears to increase by "steps" rather than in the form of a gradual change. The best example of a gradual change in the number of fossettes is in *Umbogaulus* where the later species, *U. monodon*, has fewer fossettes on the premolars than the earlier *U. galushai*. This difference is in the mean number of fossettes rather than in the range, maximum, or even minimum number. The lineage with the best evidence for a gradual increase in the number of fossettes is the one represented by species previously referred to *Mylagaulus* cf. *laevis* or *M.* cf. *monodon* from the Great Basin (Shotwell, 1958:table 2), later assigned to *Hesperogaulus* (Korth, 1999*a*). The range and mean number of fossettes in this lineage clearly increases from the early Barstovian sample (*H. gazini*) through the Hemphillian sample (*H. wilsoni*).

Within most genera, the change in the fossettes is morphological, or the change in the number of fossettes occurs in steps. For example, within the species of *Pterogaulus*, the range and mean number of fossettes on the premolars change very little from the early Barstovian *P. laevis* to the middle Hemphillian *P. cambridgensis* (Table 2), but the relative size of the fossettes does change. In the early species, the fossettes are elongated, but are no longer than about one-fourth the total length of the premolar. In *P. barbarellae* and *P. cambridgensis*, the fossettes are at least half the length of the tooth.

Evolutionary Changes in Mylagaulidae.—Even in the earliest known skulls of promylagaulines (McGrew, 1941; Nichols, 1976) many of the derived characters of mylagaulids are present: posteriorly broadened cranium with well-developed occipital crests; elongated external auditory meatus; fusion of cranial sutures early in life; enlarged last premolar; and increased hypsodonty of the cheek teeth. However, the degree of development of these features becomes much greater in the

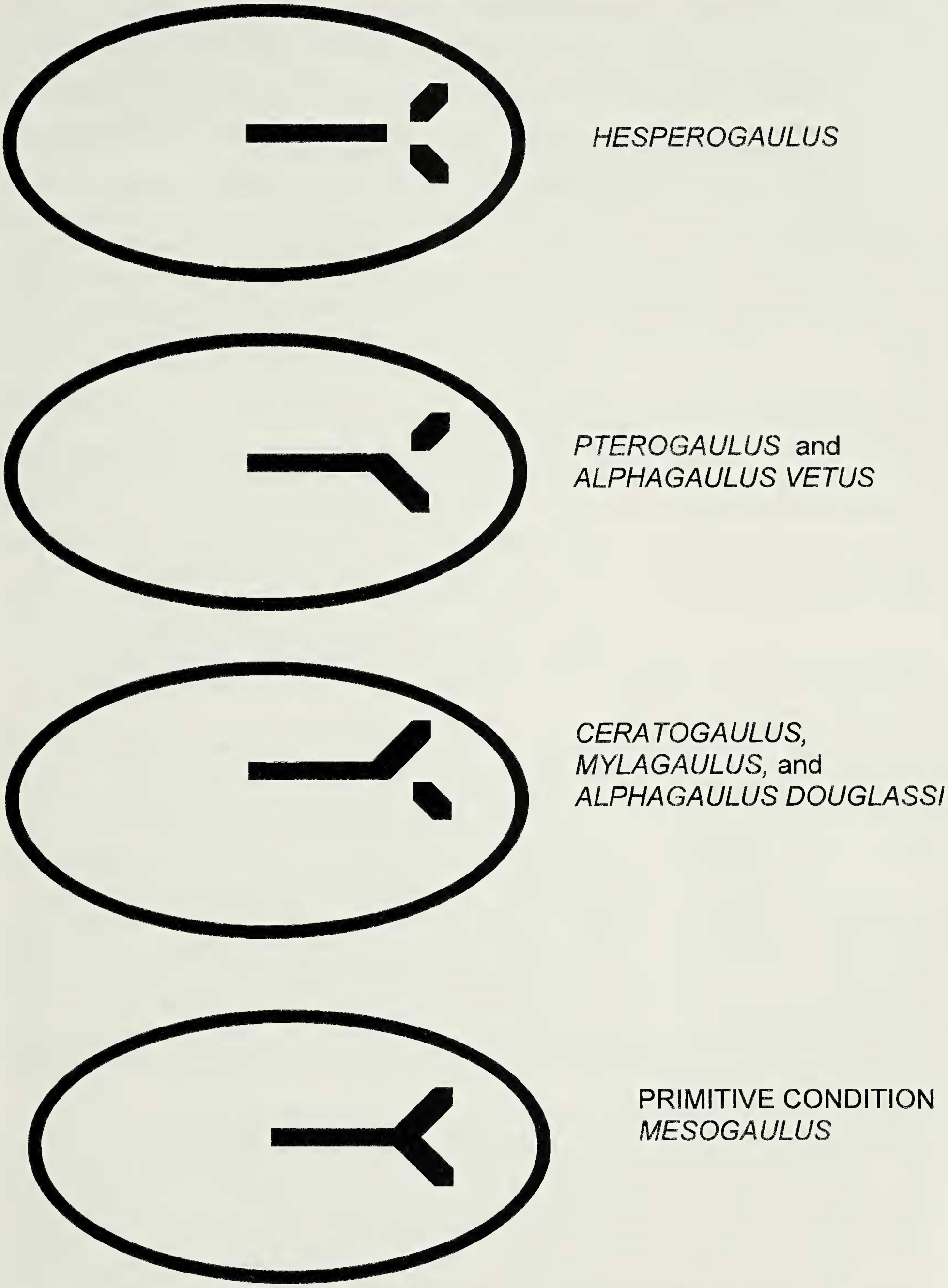


Fig. 20.—Schematic diagrams of right P^4 showing the development of the parafossette in different mylagaulids.

mylagaulines, where the cheek teeth attain nearly complete hypsodonty, anterior molars are lost with eruption of the enlarged permanent premolar, and the posterior width of the skull is nearly equal to its total anteroposterior length. *Mesogaulus* is clearly intermediate between the promylagauline condition and that of the mylagaulines. Even in the broadening of the bones of the forearm, promylagaulines appear less derived (Table 3; Korth, 1999*b*).

As in many families of mammals, there appears to be a disinct increase in size through time, with only a few exceptions. Promylagaulines are generally small species, while the majority of mylagaulines are among the largest rodents of their time. In most genera, such as *Hesperogaulus*, *Pterogaulus*, and *Ceratogaulus*, the later species are larger than the earlier species (Korth, 1999*a*; Tables 6, 7). The exception is *Mylagaulus*, which appears to decrease in size through time (Baskin, 1980).

The morphology of the cheek teeth follows a similar pattern in most genera. The mylagaulines have many more fossettes on the premolars than do promylagaulines, along with increased hypsodonty and relative size of the premolar compared to the molars. The number or relative size of the fossettes(-ids) on the premolars changes differently within different genera (see above discussion). As the relative size of the premolars increases, the number of molars lost with the eruption of the permanent tooth also increases. In promylagaulines (with the exception of *Galbreathia novellus* [Korth, 1999*b*]), P^3 and all the molars are retained in adult individuals. In *Mesogaulus*, P^3 is retained but the first molar is lost. In all mylagaulines, at least the first molars are lost with the eruption of the premolars. In advanced (Hemphillian) species of *Pterogaulus* and *Hesperogaulus*, the first two molars are shed.

Several changes have occurred in cranial morphology among mylagaulines as well. The skull of all mylagaulines has the same overall shape. The skull is posteriorly broadened with well-developed occipital crests, the cranium is relatively low, the rostrum is short, and the zygoma is robust and broad. Primitively, there are small swellings near the anterior end of the nasals. In all mylagaulids, the cranial sutures over most of the skull completely fuse early in life and are not traceable on adult individuals. The greatest changes in cranial morphology involve the modifications of the nasal bones, relative development of the postorbital processes, and the angle of the occipital. In *Alphagaulus*, the most primitive of the mylagaulines, the angle of the occipital ranges from 90°–60°, the postorbital processes are intermediate in size (POI = 0.25–0.36), and small bosses are present on the nasals. Within each lineage (genus) the changes in these features are unique to each genus.

In the short-lived lineage of *Umbogaulus*, the only modification is in the size of the bosses on the nasals. In *Umbogaulus* the bosses become very large and retain a spherical shape. The angle of the occipital and relative size of the postorbital processes remain as in *Alphagaulus*. In *Pterogaulus* the postorbital processes become greatly enlarged (POI = 0.34–0.57), the nasals are dorsally smooth (small swellings lost), and the range of the angle of the occipital is lower (OA = 52°–75°). The skull of *Ceratogaulus* develops paired horns (or horn cores) on the nasals, and the postorbital processes are greatly reduced (POI = 0.11–0.19). Within *Ceratogaulus*, the nasal horns develop progressively more posteriorly in a temporal series of species. The angle of the occipital is not as low as in *Pterogaulus* (OA = 60°–70°), but the shape of the occipital crest is modified. The primitive shape of the occipital crests for *Mesogaulus* and mylagaulines in dorsal view is that it is normal to the long axis of the skull at its center, and as it descends laterally, there is a distinct anterior flexure or bend in the crest at a point approximately one-half the distance from the center of the skull to its lateral border. However, in *Ceratogaulus*, the occipital crest is a straight line in dorsal view. The anterior bend has been lost.

The skull of *Hesperogaulus* has been modified by greatly reducing the angle of the occipital (POI = 50°) and broadening and flattening the nasals anteriorly (Korth, 1999*a*). The occipital crests on skulls of Barstovian *Hesperogaulus* are similar to those of other genera with anterior bends. However, in the Hemphillian species, the flexion is lost and the crest forms a straight line as in *Ceratogaulus*. This feature is clearly attained separately in *Hesperogaulus* and *Ceratogaulus*. It is achieved in the former as part of the decrease in the occipital angle, which pushes the anterior margin of the occipital farther anterior.

Phylogeny of the Mylagaulinae.—It is impossible at this time to determine whether any of the known Arikareean promylagaulines is directly ancestral to the later mylagaulines. It is evident that the latest of the promylagaulines (late Hemingfordian-early Barstovian) are more derived than *Mesogaulus* and are clearly not the ancestors of any mylagaulines (Korth, 1999*b*). Rensberger (1979) suggested that none of the species of promylagaulines that he studied were ancestral to later mylagaulines. However, it is likely that some unspecialized promylagauline in the late Arikareean or early Hemingfordian was morphologically transitional between the promylagaulines and *Mesogaulus*.

In the proportions of the skull and skeleton and in dental adaptations (enlargement of premolars, loss of molars), *Mesogaulus* is distinctly transitional between promylagaulines and mylagaulines. Not only are the cranial proportions intermediate between the latter two subfamilies, but the dentition is also similar to that of mylagaulines and advanced over promylagaulines in some characters (loss of molars), but similar to promylagaulines and more primitive than mylagaulines in others (retention of P^3). There is nothing in the morphology of *Mesogaulus* that would exclude it from the ancestry of all mylagaulines (Fig. 21).

Within the Mylagaulinae, *Alphagaulus* is the earliest (late Hemingfordian-early Barstovian) and most primitive genus. This is evidenced by the proportions of the skull, presence of a small boss on the nasals, and angle of the occipital (Table 1), as well as the relatively fewer number of fossettes(-ids) on the premolars (Table 2). At least two of the later lineages (genera) of mylagaulines can be derived from species of *Alphagaulus*. Both *A. vetus* and *A. pristinus* have relatively gracile skulls and separate the buccal fork of the parafossette on P^4 with wear. These characters can be traced to species of *Pterogaulus* and even possibly species of *Hesperogaulus* (Korth, 1999*a*). *Alphagaulus douglassi* and *A. tedfordi* have more robust skulls, a larger nasal boss, and separate the lingual fork of the parafossette on P^4; characters found in *Ceratogaulus* and *Mylagaulus*. Besides *Alphagaulus*, five genera appear in the Barstovian. The earliest is *Umbogaulus*, which is restricted to the Barstovian. This genus is generally primitive cranially, but develops a much larger boss on the nasals than do species of *Alphagaulus*. Dentally, this genus is far advanced over the other genera of the Barstovian in the much greater number of fossettes on the premolars. *Umbogaulus* is short-lived, restricted temporally to the Barstovian, and clearly not ancestral to any other. The only character that might relate *Umbogaulus* with any other genus is the enlarged bosses on the nasals, which are more similar to the nasal horns of

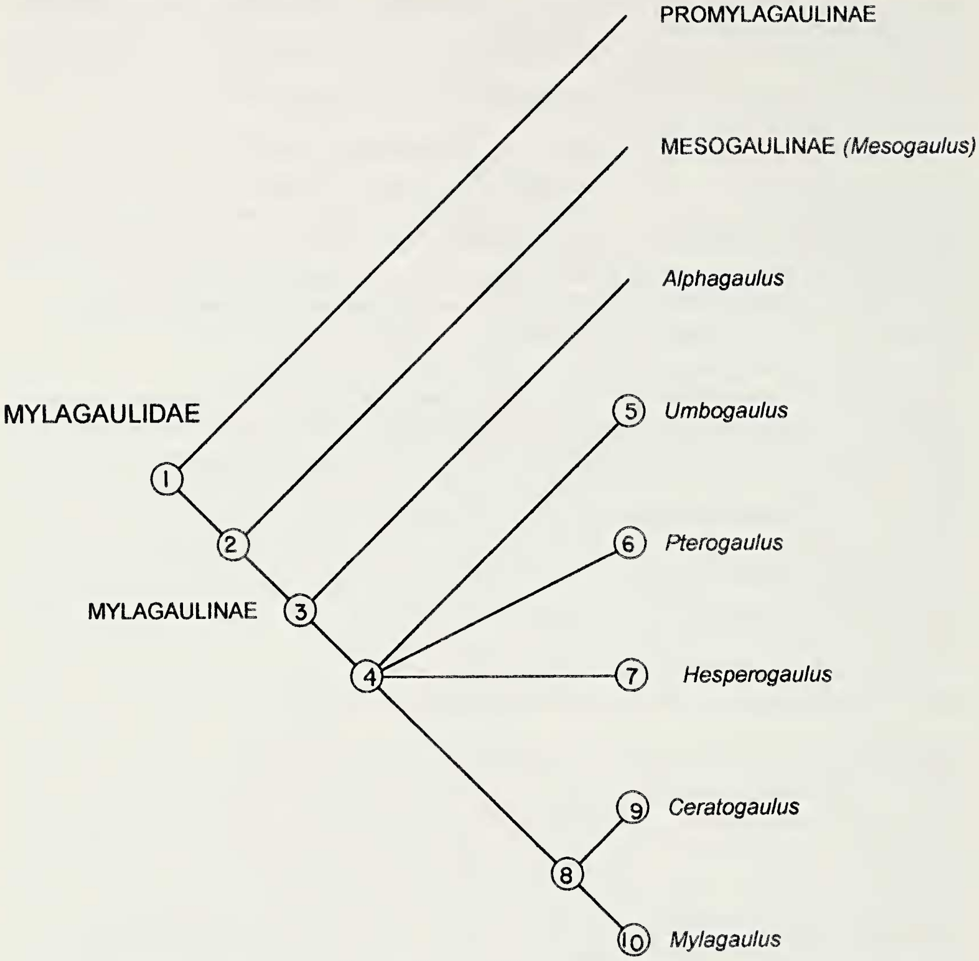


Fig. 21.—Cladogram of relationships of mylagaulids. Explanation of nodes: **1.** Mylagaulidae: protrogomorphous zygomasseteric structure; uniserial microstructure of incisor enamel; incisors broadened; low, broad, robust skull with heavy occipital crest and shortened rostrum; postorbital process present on frontals; cranial sutures completely fuse relatively early; auditory bulla with elongated external meatus; postcranial skeleton fossorially adapted; last premolars largest cheek teeth; cheek teeth lophate, occlusal pattern reduced to isolated enamel "lakes" (cusps reduced); cheek teeth progressively hypsodont. **2.** Larger size; posterior width of skull subequal to anteroposterior length; postcranial skeleton fossorially adapted (humeral index $\geq$ 0.40); first molars lost with eruption of permanent premolars; premolars at least twice the size of molars. **3.** Mylagaulinae: P^3 lost; broad, shallow groove on upper incisor; greater number of fossettes(-ids) on premolars (minimum number and six for P^4, five for P_4); premolars completely hypsodont (roots lacking); small paired bosses on anterodorsal end of nasal bones; double sagittal crest. **4.** Largest mylagaulids; premolars nearly oval in occlusal outline (loss of outline of stylar cusps); occipital anteriorly tilted (OA $\leq$ 90°). **5.** *Umbogaulus*, nasal bosses greatly enlarged; number of fossettes(-ids) on premolars increased ($\bar{x}$ = 8–9); upper premolars wider relative to length than other mylagaulines. **6.** *Pterogaulus*, postorbital processes greatly enlarged (POI = 0.35–0.54); bosses on nasals lost; buccal fork of parafossette of P^4 separates first; premolars narrower relative to length than in other mylagaulids. **7.** *Hesperogaulus*, angle of occipital lower than other mylagaulids (OA = 50–57°); bosses on nasal bones low and anteriorly broadened and squared-off; either of the anterior branches of forked parafossette of P^4 may separate first. **8.** lingual fork of parafossette on P^4 separates first; premolars wider relative to length than in *Pterogaulus*. **9.** *Ceratogaulus*, horns (horn cores) on nasal bones; postorbital process progressively reduced

Ceratogaulus than to the condition in any other genus. Again, the premolars of *Umbogaulus* are too complex to have been ancestral to *Ceratogaulus*.

A second lineage of mylagauline is represented by *Pterogaulus*. This genus is restricted to the northern Great Plains and is characterized by the loss of nasal bosses and enlargement of the postorbital process. It ranges from the Barstovian to the medial Hemphillian. Dentally, it can be distinguished by the separation of the buccal fork of the parafossette on P^4, which occurs at a progressively earlier wear stage in later species. This lineage shows through time an increase in skull size and proportional size of the premolar, increased size of the postorbital process, and increased length of the fossettes on the premolars.

Ceratogaulus is restricted temporally and geographically to the same time span as *Pterogaulus*, and they are often found in the same faunal horizons. It, too, shows a distinct increase in size over time along with the more posterior postition of the nasal horns and reduction of the postorbital process (Table 1).

A fifth genus, *Hesperogaulus*, from the Great Basin, originates in the Barstovian and exists until the Hemphillian, and exhibits an increase in size as well as complexity of the premolars (Korth, 1999*a*).

Biogeography of the Mylagaulinae.—Promylagaulines appear in the fossil record during the Arikareean and are limitied geographically to the northern Great Plains and Rocky Mountains (McGrew, 1941; Nichols, 1976; Rensberger, 1979, 1980; Korth, 1992). In the early Hemingfordian, species of *Mesogaulus* appear in approximately the same area (Riggs, 1899; Galbreath, 1953; Wilson, 1960). By the late Hemingfordian, the first mylagaulines appear alongside advanced promylagaulines, again limited to the northern Great Plains and Rocky Mountains. During the Barstovian the remainder of the genera of mylagaulines appear. Three of these genera (*Umbogaulus*, *Pterogaulus*, and *Ceratogaulus*) are limited geographically to the northern Great Plains. However, another distinctive lineage, *Hesperogaulus*, appears in the northern Great Basin (Shotwell, 1958; Korth, 1999*a*). The more primitive mylagaulines (*Alphagaulus* and *Umbogaulus*), along with the specialized promylagaulines (Korth, 1999*b*), do not survive the end of the age. The Clarendonian and Hemphillian occurrences of the four surviving genera show a distinct geographic isolation that began in the Barstovian. *Hesperogaulus* continues into the Hemphillian in Nevada and Oregon (Shotwell, 1958; Korth, 1999*a*). Clarendonian and Hemphillian species of *Mylagaulus* are known only from Florida (Webb, 1966; Baskin, 1980), even though this lineage probably originated in the Great Plains alongside two other genera, *Ceratogaulus* and *Pterogaulus* in the Barstovian or Clarendonian. The latter two genera are completely restricted to the northern Great Plains throughout their fossil records.

The geographic distribution of the species of mylagaulids (Fig. 22) suggests a number of conclusions. First, the origin and early radiation of the family was within the northern Great Plains and Rocky Mountains. Then, with the rapid diversification of mylagauline genera beginning in the Barstovian, there is a geographic dispersal of these genera with one lineage migrating to the Great Basin

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(POI = 0.24–0.11); occipital crest more robust than in other mylagaulines and forms straight transverse crest (no anterior bend on either side as in other mylagaulines); anterocentral fossettid on P_4 V-shaped in early wear (apex pointed posteriorly), lingual branch separates in early wear. **10.** *Mylagaulus*: posterobuccal fossette on P^4 C-shaped; reduction in size and complexity of premolars.

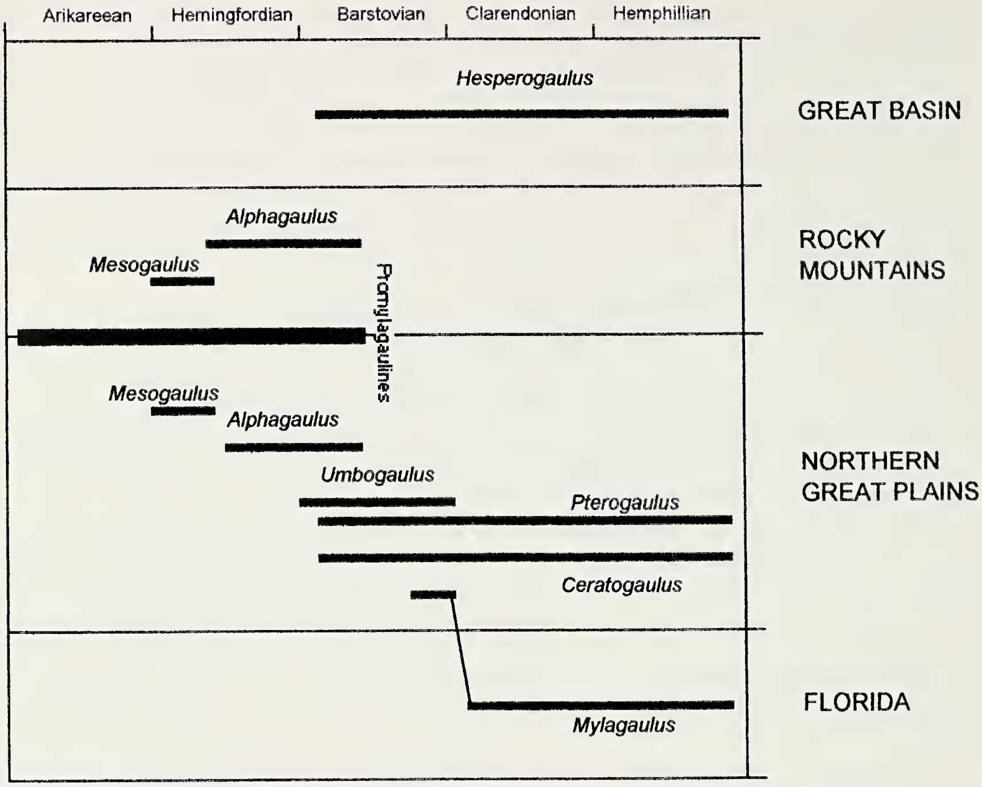

Fig. 22.—Biostratigraphic and geographic occurrence of mylagaulids.

(*Hesperogaulus*) and another to Florida (*Mylagaulus*). Only two lineages remain in the Great Plains until the end of the Hemphillian.

Among the specimens of the AMNH Frick collections are a number of mylagaulids from the Barstovian of New Mexico and the Hemphillian of Texas. These specimens were not included in this study; however, the New Mexico material may represent yet another morphologically and geographically distinct lineage. This lineage cannot be directly related to the Texas material from the Hemphillian at this time, but may prove to be related taxa.

Sexual Dimorphism.—In his initial description of *Ceratogaulus rhinocerus*, Matthew (1902) suggested that the horns on the nasals of this species were possibly a sexually dimorphic character, and that the skull of "*Mylagaulus*" *laevis*, from the same horizon which lacked horns, was the skull of a female individual. He rejected this idea (Matthew, 1902, 1924) mainly because there was no known example in rodents, Recent or fossil, that had this scale of dimorphism. It is now evident, with the discovery and description of numerous mylagaulid skulls, that the horns on the skulls of species of *Ceratogaulus* are a distinctive generic character and not a sexual one due to the fact that other cranial characters (size of postorbital processes) and dental characters (morphology of parafossette on P^4 and anterocentral fossettid on P_4) clearly separate the horned mylagaulids (*Ceratogaulus*) from the hornless mylagaulids (*Pterogaulus*) of the Great Plains.

However, in one lineage of mylagaulines there may be sexual dimorphism. In the species of mylagaulids from the Great Basin, cited by Shotwell (1958) that were later referred to *Hesperogaulus* (Korth, 1999*a*), there appears to be a difference in the relative robustness of the skulls of individuals with no evidence of a difference in dental dimensions or morphology. Skulls of *H. gazini* from the Barstovian and *H. wilsoni* from the Hemphillian of Oregon (Korth, 1999*a*) are divisible into larger and smaller sizes, suggesting a dimorphic condition. In no other species is there even a suggestion of sexual dimorphism. However, this disparity in size of skulls in *Hesperogaulus* may be due to the lack of an adequate sample for comparison.

Problematical Species.—There are examples of specimens or species of mylagaulids that are not clearly assignable to known genera or lineages of mylagaulids. These include *Mylagaulodon* and a pair of unusual specimens from the Clarendonian of Oregon.

Mylagaulodon angulatus was first named by Sinclair (1903) from the Hemingfordian of Oregon, and was believed to represent a transitional form between meniscomyine aplodontids and mylagaulids. Matthew (1924) argued that the premolars of the holotype of *M. angulatus* (UCMP 1652) were deciduous teeth and that the specimen was a juvenile of *Mylagaulus*. Despite Matthew's suggestion, later authors continued to consider *Mylagaulodon* as the basal mylagaulid (McGrew,1941).

Subsequent identifications of specimens of *M. angulatus* from the Great Plains (McGrew, 1941; Skwara, 1988) appear to be specimens of other mylagaulids (Korth, 1992:91). Korth (1992) suggested that *M. angulatus* represented an advanced meniscomyine aplodontid rather than a mylagaulid, later questionably including *M. angulatus* in the Meniscomyinae (Korth, 1994). Whether the type of *Mylagaulodon* is an advanced meniscomyine or a juvenile mylagaulid cannot be determined at this time. However, it does appear that it does not represent a species transitional between the mylagaulids and an aplodontid ancestor as had been previously suggested.

Shotwell (1958:fig 13) identified two isolated P^4s from the Clarendonian of Juntura Basin as *Epigaulus minor* (UOMNH F6165, F6166). Later, he (Shotwell and Russell, 1963) suggested that these two premolars were from the same individual. These two specimens are unique among all described mylagaulids. The fossettes are unusually branched and there is a deep reentrant valley along the buccal side of the tooth that is reminiscent of the mesoflexus of the upper cheek teeth of beavers. These specimens clearly belong to a mylagaulid, but do not fit into any genus recognized at the present time. These specimens should be considered as belonging to an indeterminate mylagaulid.

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APPENDIX 1

Cranial measurements of mylagaulid specimens examined in this study (see Figure 1 for orientation of measurements). Abbreviations for cranial measurements: L, length; PW, maximum posterior width; POC, minimum postorbital constriction; POP, length of postorbital process; OA, angle of the occipital with the plane of the palate; NL, horizontal distance of the apex of the nasal horn from the anterior end of the nasals (*Ceratogaulus* only). All measurements in mm. Asterisk indicates approximate measurement.

Specimen	L	PW	POC	POP	OA	NL	Horizon
Mesogaulus paniensis							
FAM 65511	48.05	39.5	11.05	4.05	90°	—	Marsland Fm., NE
Alphagaulus vetus							
AMNH 18903	—	51.2	14.1	4.3	—	—	Sheep Creek Fm., NE
AMNH 20507	58.7	51.6	15.4	4.9	75°	—	Sheep Creek Fm., NE
FAM 65515	62.5	50.1	14.6	—	60°	—	Sheep Creek Fm., NE
FAM 65532	62*	51.5	15.8	5.8	70°	—	Observation Quarry, NE
FAM 65533	—	—	16.2	4.1	—	—	Observation Quarry, NE
Alphagaulus pristinus							
AMNH 21307	—	22.65	11.20	3.50	79°	—	"Deep River Beds," MT
Alphagaulus tedfordi							
FAM 65711	64.7	78.8	14.60	3.60	90°	—	?Hemingfordian, NE
Umbogaulus monodon							
FAM 65016	79.3	69.35	20.00	7.10	75°	—	Olcott Fm., NE
Ceratogaulus rhinocerus							
AMNH 9456	66.7	70.6	17.50	4.55	70°	9.85	Pawnee Creek, CO
FAM 65815	—	—	23.75	4.20	—	—	Crookston Bridge Mb., NE
FAM 65014	—	—	—	—	—	19*	Devil's Gulch Mb., NE
FAM 65015	—	57.4	—	—	—	—	Devil's Gulch Mb., NE
FAM 65802	—	66.8	—	—	—	—	Devil's Gulch Mb., NE
FAM 65012	70.7	60.3	16.60	2.05	—	12*	Burge Mb., NE
FAM 65013	—	67.8	—	—	68°	—	Burge Mb., NE
FAM 65385	79.35	70.0	17.40	2.15	67°	17.40	Burge Mb., NE
FAM 65833	—	70.4	17.00	2.50	—	—	Burge Mb., NE
FAM 65489	76.2	60.7	18.00	2.40	—	18.30	Burge Mb., NE
Ceratogaulus anecdotus							
FAM 65466	63.0	63.0	17.25	2.12	—	17.5	Cap Rock Mb., NE
Pterogaulus laevis							
AMNH 17576	58.0	56.0	12.45	5.40	—	—	Olcott Fm., NE
FAM 65471	63.6	52.4	12.00	5.85	—	—	Olcott Fm., NE
Pterogaulus sp.							
FAM 65008	67.35	56.2	19.30	6.60	57°	—	Burge Mb., NE
FAM 65009	—	54.5	15.80	5.95	54°	—	Burge Mb., NE
FAM 65010	—	55.0	17.60	6.15	55°	—	Burge Mb., NE
FAM 65470	66.5	59.8	19.00	7.90	48°	—	Cap Rock Mb., NE
Pterogaulus barbarellae							
FAM 65435	67.9	61.6	17.40	8.90	—	—	Merritt Dam Mb., NE
FAM 65436	—	—	16.70	9.50	—	—	Merritt Dam Mb., NE
FAM 65491	72.9	63.3	18.60	9.30	52°	—	Merritt Dam Mb., NE
FAM 65499	69.2	73.0	19.90	9.05	52°	—	Merritt Dam Mb., NE

APPENDIX 2

Classification of Mylagaulidae included in this paper

- Family Mylagaulidae Cope, 1881
  - Subfamily Mesogaulinae, n. subfam.
    - *Mesogaulus* Riggs, 1899
      - *Mesogaulus ballensis* Riggs, 1899
      - *Mesogaulus paniensis* (Matthew, 1902)
  - Subfamily Mylagaulinae Cope, 1881
    - *Alphagaulus*, n. gen.
      - *Alphagaulus vetus* (Matthew, 1924)
      - *Alphagaulus pristinus* (Douglass, 1903)
      - *Alphagaulus douglassi* (McKenna, 1955)
      - *Alphagaulus tedfordi*, n. sp.
    - *Umbogaulus*, n. gen.
      - *Umbogaulus galushai*, n. sp.
      - *Umbogaulus monodon* (Cope, 1881)
    - *Mylagaulus* Cope, 1878
      - *Mylagaulus sesquipedalis* Cope, 1878
      - *Mylagaulus kinseyi* Webb, 1966
      - *Mylagaulus elassos* Baskin, 1980
    - *Ceratogaulus* Matthew, 1902
      - *Ceratogaulus rhinocerus* Matthew, 1902
      - *Ceratogaulus hatcheri* Gidley, 1907
      - *Ceratogaulus minor* (Hibbard and Phillis, 1945)
      - *Ceratogaulus anecdotus*, n. sp.
    - *Pterogaulus*, n. gen.
      - *Pterogaulus laevis* (Matthew, 1924)
      - *Pterogaulus cambridgensis* (Korth, 2000)
      - *Pterogaulus* sp.
      - *Pterogaulus barbarellae*, n. sp.